ABSTRACT

Title of Dissertation: ON THE DEVELOPMENT OF POSTURAL STABILITY DURING INFANCY AS A PROCESS OF GROWTH AND ACTIVE, EXPLORATORY SENSORIMOTOR TUNING

Jason S. Metcalfe, Doctor of Philosophy, 2007

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The process by which humans stabilize bipedal stance represents a confluence of changes associated with musculoskeletal maturation and experience-based sensorimotor learning. While investigations have documented a variety of changes with increased bipedal experience, such as reduced velocity and frequency of postural sway and concomitant refinements in muscle activation sequences, the extent to which these changes may be ascribed to growth versus learning processes has not been well characterized. For example, reduced sway frequency is a natural consequence of increasing body height but alternatively, may be explained by active modulations in motor commands specifying the timing and magnitude of muscular activation sequences. It is clear that both types of influences are needed to explain postural development. However, a parsimonious framework for understanding and explaining postural development has yet to be clearly articulated *and* validated against empirical observations. As such, the purpose of this dissertation was to initiate the development of such an account through a combination of empirical and computational studies.

In this dissertation, data are presented from a longitudinal study of upright posture in infants ranging from the onset of independent sitting until 9 months of walking

experience; this dissertation focused on the particular period spanning from walk onset onward. Infants participated in a quiet stance task involving hand contact with a surface that was either static or dynamic as well as an independent stance condition. Empirical analyses were performed to estimate the statistical properties of sway and characterize adaptations to static and dynamic manipulations utilizing the touch surface. An unexpected lack of significance for sway magnitude was observed in all conditions. Robust effects, however, were found across measures of rate properties of sway. Taken in the context of previous literature, the empirical observations were used to guide a final study utilizing computational techniques to test hypotheses regarding potential sources of change in postural development. First, the mechanical and computational requirements for postural stabilization were systematically assessed through a review of extant models of both stance and motor learning. Armed with insights from this review, the final study examined an autonomous reinforcement learning algorithm, that was designed to capture the essence of how a human may stabilize his or her posture under the tutelage of exploratory action. Simulation results provided evidence in support of conclusions regarding changes in rate-properties of postural sway and underlying associations with physical growth as well as calibration of both sensory and motor system parameters. Further, simulations emphasized the importance of inclusion of noise in biologically-relevant aspects of the model, such as in sensory and motor processes, as well as the need to consider physical morphology as a primary constraint on sensorimotor learning in the context of upright postural development.

ON THE DEVELOPMENT OF POSTURAL STABILITY DURING INFANCY AS A PROCESS OF GROWTH AND ACTIVE, EXPLORATORY SENSORIMOTOR TUNING

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Dissertation submitted to the Faculty of the Graduate School of the
University of Maryland, College Park in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
2007

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Dedication

To Dennis B. Metcalfe (1943 – 2001), who ceaselessly facilitated the achievements of his family and encouraged the continual expansion of their intellectual and rational abilities.

Acknowledgements

There are many, many people that should be thanked for their roles as teachers, mentors, colleagues, advocates, friends, family, sounding boards, and sources of support, encouragement and continued challenge as I have gone through the doctoral process.

I extend special appreciation to the members of my dissertation committee: Jane E. Clark, John J. Jeka, José L. Contreras-Vidal, Tim Kiemel and Amanda Woodward. You were all incredibly patient in guiding me through this process.

Beyond her role as my academic advisor, I want to express my fullest gratitude to Jane E. Clark for her role as my mentor. Jane has supported me through as many years as I could ask . . . and then some! Not only has her support been limitless, but her encouragement, demands and provision of developmental opportunities have all brought out potential within me that I never thought existed. In addition to Jane's indispensable mentoring, I must also acknowledge the fundamental influence of my M.S. advisor, Karl S. Rosengren (University of Illinois), without whom I would have never gotten my start in science.

In addition to my direct advisors, I have been honored to attend classes, seminars, conferences and even a few happy hours with a great many scholars including: John J. Jeka, Jill Whitall, José L. Contreras-Vidal, Tim Kiemel, Sally J. Phillips, J. Paul Boudreau, Bradley Hatfield, Les Carlton (U. of Illinois), Mary Carlton (U. of Illinois), Larry Douglass and C. Mitchell Dayton. Each of these has contributed in their own unique ways to my understanding of the science of human cognitive-motor behavior.

Of course, only a portion of graduate education happens in formal settings such as the laboratory and classroom. These formal lessons, however, would not be nearly as influential if one did not have compatriots, colleagues and friends with whom they could discuss, debate and occasionally commiserate. While I am certain to leave a few names off of the list, as there have been *many* whom I want to thank.

From the Department of Kinesiology: Li-Chiou Chen, “Disco” Steve Kim, Ewout Meijer, Pedro Ribeiro, Rob Creath, Ethan Buch, Scott Kerick, Tzu-Yun Chang (now Chang-McDowell), Woei-nan Bair, Melissa Pangelinan, Brad King, Jo Zimmerman, Ron Goodman, Jeremy Reitschel, Marcio Oliveira, Gwyneth Dickey, Jim Dana, Leslie Allison, Jin Bo, Elaine Henson, Kristine “Crash” Leonard, Chuck Hillman, Minjung Woo, Shu-Chen Lee, Jamal Wakeem, Tim Benson, Youngsoo Lee and Ryan Conery;

From my associations through the program in Neuroscience and Cognitive Science and elsewhere at UMD: Chris Peratino, Dave Boothe, Beth Stevens, Todd Roberts, Jen Holdway, and Shiva Sinha;

The following two individuals deserve distinct recognition as my “intellectual older brothers”, without whom I would never have achieved the ability to think about science in the ways that I can today: Kaleb McDowell and Kelvin S. Oie.

While I do not acknowledge them nearly enough, the members of my extended family have all been essential to making this possible. To the “Aurora family” - Doug, Denise, Chris, Carolyn, Dean, Sue, Josh, Justin, Dianna, Gary, Deb, Jen, Adam, Dee, David, Claire, Kathy, Donna, Dennis; and the “Chicago family” - Laurie, Jessie, Jodi, Evelyn, Al, Pat, Adam, Carolyn, Brian, Debbie, Beth - you are all the best!

To my immediate family, Dale, Arlene, Ryan, Sandi and Matthew, you know that there is no way I could have made it through all of this without your love and prayers. And, of course, to my grandparents Ted, Jean, Clara & Norris – if only this could have been done in time for you to share in the pride.

Finally, to the person who has become the central inspiration in my life in the last 3 years, Nisha Isaac, thank you, for being my friend, my support, my confidant and my love.

The research in this dissertation was supported by: The Department of Kinesiology, The University of Maryland Dissertation Fellowship and NSF Grant #9905315 (P.I. Jane Clark).

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Chapter 1

Introduction

From the buckling knees and unsteady feet of infants, to effortless and graceful sauntering through crowded streets as adults, our postural and locomotor abilities are dramatically transformed throughout our lives. Seen as fundamental to a majority of motor skills, the ability to maintain an upright posture in and safely navigate through complex environments is a capacity that we, as adults, generally take for granted. However, for the infant attempting to take his first steps, learning to manage a complex, multi-segmented body in order to remain upright while traversing even the simplest surfaces represents no trivial problem. This problem, the acquisition and stabilization of upright bipedal posture, is thus the focus of this dissertation.

The complexity of simplicity: Postural development

Although it takes approximately a year for the infant to first attempt independent walking, a short 3 months later she consistently produces the fundamental pattern of interlimb co-ordination that characterizes adult locomotion (Clark et al., 1988; Clark & Phillips, 1987; Clark & Phillips, 1993). Six months after walking onset, the infant produces this same pattern of co-ordination with enough force and consistency to generate her first running movements. During this same period, she decreases the magnitude of her upper body sway corrections (Ledebt & Bril, 2000; Metcalfe & Clark, 2000), stabilizes muscle activation sequences in response to both sensory and mechanical perturbations (Hirschfeld & Forssberg, 1992; Sveistrup & Woollacott, 1996), and begins to use more complicated multi-joint patterns of postural co-ordination (McCollum & Leen, 1989). To temper our enthusiasm for these remarkable achievements, we note that

this progression takes a tremendous amount of time in comparison with the vast majority of the animal kingdom. While many species are capable of locomotion within hours, days or weeks following birth, during the first few months of life the human infant will struggle even to lift his own head and, further, will not sit independently until approximately the 5th or 6th postnatal month. More remarkably, for most typically developing humans, the first sequence of about 3 -5 independent steps is not seen until roughly the end of the first year.

When one considers the mechanical constraints imposed by the human body on maintenance of a bipedal posture, it becomes less perplexing as to how standing and walking emerge over such a protracted period. For example, the dominant size of the upper body relative to the lower limbs in the early postnatal months results in a center of mass located approximately mid-trunk (Palmer, 1944) thus precluding, or at least making rather difficult, the ability to achieve and maintain an upright position. At the same time, it is reasonable to conclude that there is more to the story than simply a changing physical structure, particularly when discussing postural development following the onset of independent walking when the rate of physical growth has dropped to about half of what it was in the first year (Malina et al., 2004). While shifts in the body mass distribution with growth and maturation establish a more favorable mechanical basis for bidepdalism, they do not fully capture the significant contributions of active neuromuscular control processes that also change as the human infant learns how her body is to work in our terrestrial environment.

Among the variety of reasons to entertain explanations of postural development that include active neuromuscular contributions are robust observations of broad

behavioral changes associated with apparently discrete transitions in postural and locomotor status. For example, research to date has established clear links between the emergence of self-produced locomotion, most commonly the onset of hands-and-knees crawling, and changes in fear of heights, the relative use of body-centered versus environment-centered cues for spatial localization tasks, the influence of optic flow field properties on standing and finally, the dynamics of the mother-infant dyadic relationship (c.f. Anderson et al., 2001; Bertenthal et al., 1994; Campos et al., 2000 for review). A growing body of studies provides compelling evidence that such behavioral reorganizations are not confined to the emergence of any particular instantiation of self-produced locomotion, such as hands-and-knees crawling, but can instead be seen in association with other postural and locomotor transitions. As a somewhat dated, yet excellent example, it was shown that new capabilities for asymmetric bimanual coordination emerged concomitant with the ability to sit independently (Rochat, 1992).

Similarly to self-produced locomotion, the transition to independent walking has been associated with a broad array of functional changes including: prospectivity in the use of somatosensory information (Barela et al., 1999), transient destabilization of the already well-practiced behavior of sitting (Chen et al., 2007b), the relative frequency of uni- versus bimanual reaching (Corbetta & Bojczyk, 2002), memory for spatial navigation tasks (Clearfield, 2004) as well as specific changes in sensory modalities such as the differential role of canal versus otolith signals in the vestibular system (Wiener-Vacher et al., 1996). Indeed, to the extent that the physical structure of the body is in a state of rapid growth, one would expect to see relatively broad manifestations in behavioral change. However, the types of changes that may be attributed to changing

morphology alone do not have an intuitive connection with the range of changes described above, particularly those dealing with social and cognitive tasks. As such, in our quest to understand human postural development, we seek a process that has an intuitive, although not necessarily direct, connection with the variety of behavioral changes associated with dramatic developmental transitions in motor behavior.

Sensorimotor integration and its consequences for motor development

Previously, we have articulated our theoretical stance regarding the teleology of human development; that is, we believe that the end-goal of development resides in the process itself (Clark & Metcalfe, 2002). This view is consistent with others who have considered the process of development as one in which the individual attempts to acquire and maintain a repertoire of behaviors that facilitates survival within the environment of their rearing (see Charlesworth, 1986 for discussion). In human behavior in particular, such adaptability is considered a hallmark of skillfulness and thus, it can be said that progress towards, and the subsequent maintenance of, skillfulness is an essential driving force behind human development (Bruner, 1973; Clark, 1995; Clark, 1997; Hofsten, 1997; Thelen, 2000a; Thelen, 2000b). The system-wide consequences associated with postural and locomotor transitions imply the involvement of 'domain-general' processes that underlie the changes observed in behavior across ontogeny. Skillful behavior requires well-integrated sensory and motor functionality in order to be maximally adaptive and, as such, we suggest that a particularly good candidate for investigation is the fundamental coupling between sensory-perceptual information and overt motor behavior. In other words, for the domain of skillful, sensorimotor behavior, we look to a generalized notion of 'sensorimotor integration' as an important underlying process.

Indeed, studies of both postural and locomotor development have documented considerable changes in motor performance that are linked to the dynamics of the surrounding sensory-mechanical context (Barela et al., 1999; Bertenthal et al., 1997; Butterworth & Hicks, 1977; Delorme et al., 1989; Foster et al., 1996; Gibson & Schmuckler, 1989; Lee & Aronson, 1974; Metcalfe & Clark, 2000; Schmuckler & Gibson, 1989; Stoffregen et al., 1987). However, what these studies have left largely unexplored is how sensorimotor relationships are tailored to the biologic milieu within which they are embedded. That is, considering that the human infant is establishing sensorimotor relations while her body remains in a state of continual physical change, it is necessary to understand the implications of a changing physical structure on both the outcome and the process of sensorimotor learning.

Outcome implies process?

One outcome that we, as well as others (Bertenthal, 1996; Bertenthal & Clifton, 1998; Clark, 1997; Hofsten, 1997), consider important is that of prospective control. Here it is considered that prospective control emerges out of necessity due to the physical, inertial properties of the human body and further, from the proper use of different aspects of sensory information. Humans must have a capacity to account for the mechanical properties body, as well as known transmission delays within the sensorimotor system, before they select an action that may negatively influence achievement of a given task goal. Without the ability to predictively assess the consequences of an action to be executed within a particular sensory-mechanical context, most people would frequently fall prey to slippery surfaces, run headlong into closing doors and make embarrassing exits off escalators. Following the notion of emergent prospective control leads to

questions of process. That is, by which process does the human sensorimotor system learn to attend to and utilize various aspects of the sensory array differentially depending on task and context? More directly: how do humans develop, refine and maintain adaptive sensorimotor relationships?

A common answer to this question is that sensorimotor relationships can be learned through active exploration of movement and its consequences (Adolph et al., 1993; Adolph, 1997; Adolph, 2000; Gibson, 1987; Metcalfe & Clark, 2000). Human action is remarkably plastic and the skilled human easily tailors her actions to various task and environmental contexts. The consequence of this adaptability is that it makes the process of development seem a rather capricious enterprise. In order to have such flexibility in our behavioral repertoire, a developmental process is needed that relies less on innate reflexes and pre-determined 'sensory-to-motor maps' and more on an epigenetic mechanism of skill acquisition. As mentioned above, one such process that has been advocated is that of active exploration, which allows a particular individual to adapt the constraints defined by her specific body to those of the broader environmental context within which she is embedded.

Unfortunately, while the literature claiming to support hypotheses regarding the relationship between active exploration and sensorimotor adaptation is growing rapidly, the explanations posited to date have been, at best, speculative. That is, despite significant theorizing and phenomenological observation, questions remain about how, in a mechanistic sense, exploratory action facilitates the development of adaptive sensory-motor relationships. For example, one may ask what connection, if any, exists between an early movement and successive improvement in that same movement? How does

sensory-perceptual information become an integral part of movement control? If this integration, or coupling, is present from birth, what is its nature and how does it appear and/or differ across ontogeny (Thelen, 2000a)? In the case of this dissertation, when a developing human 'explores' postural behavior, what information is gained from that exploration and how is it used to make modifications to stance control behavior?

Statement of purpose and dissertation structure

Part of the problem in answering the difficult questions about sensorimotor development is often in how they have been asked. That is, the difficulty in arriving at sufficient answers is, in part, due to a gap in communication between those most closely studying the problem. Indeed, postural development has been widely studied by many with diverse scientific approaches, including, for example, those who utilize verbal, construct-based theoretic perspectives, those whose biases draw their attention to neurophysiologically- and/or neuroanatomically-motivated interpretations and, finally, those who adopt mathematical or engineering-based schemes for evaluating and explaining the development of complex human behaviors. While each of these 'camps' of investigators has contributed and continues to contribute unique information to the overall comprehension of postural development, each is also challenged in unique ways because of inherent limitations on the knowledge *within* any given domain of specialization.

Through this dissertation, we set out to join those who are working to rectify this communication gap (c.f. Berthier et al., 2005; Mareschal, 2000; Metta et al., 1999; Shultz, 2003). By synthesizing insights from several domains, such as motor development, computational neuroscience, biomechanics, control systems engineering

and psychology, we intended to advance the current understanding of the processes contributing to the stabilization of human postural behavior during early development. Specifically, this dissertation is focused on the robust relationship between postural (and locomotor) experience and changes in postural sway during infancy. Analyses of longitudinal data on human postural sway that were recorded during the second year of life were combined with expressions of the problem of postural control in computational terms in order to identify a plausible set of physical and computational principles sufficient to instantiate functional adaptations in the developing infant. The overall objective, therefore, was to develop a precise understanding of the interaction between the various types of constraints on human postural development.

In what follows, the examination of postural development is opened in chapters 2 and 3 by the presentation of empirical studies that characterized developmental changes in posture within stationary conditions as well as a dynamic quiet stance task. The purpose of presenting these studies first was to embellish the extant literature by providing a solid empirical basis against which later theoretical work could be compared (Chapter 5). Following the empirical studies, Chapter 4 provides an overview of the current state of knowledge on postural control as well as the refinement of sensorimotor relations as examined in the context of computational studies of human motor development. The overview was organized in two major sections. In the first of these sections, we systematically 'built' a model-based understanding of the major constraints on upright postural control. Following that discussion, we then mapped known developmental changes onto the computational models in order to hypothesize specific sources of change in infant postural control. In particular, we considered morphologic

changes in the human body across the first two years of life, including whole-body growth as well as shifts in mass distribution and proportionality. Some elements of muscular development, such as postnatal changes in fiber size, fiber type distribution and metabolic properties, are discussed in relation to where and how such information may inform developmental modeling efforts. However, an assessment of the current state of the literature regarding muscular development during infancy indicated that available information was too incomplete to afford making any conclusive statements beyond broad theoretical discussion. Through this review we motivated the selection of the model employed in the final study of this dissertation. The specific goals of the final study were two fold. First, we aimed to provide a clear picture of how use of models may facilitate the development of a precise understanding of the interaction of constraints that brings about human postural stability. Second, and equally as important, we wished to assess a current and popular model of learning in terms of its ability to capture the essence of actual human development. That is, in this examination, not only was the model used to assess and interpret empirical observations, but the empirical observations were used as a barometer of the relative fidelity of the model with respect to replicating human-like behaviors during postural development.

In the fifth chapter, therefore, we present a simulation study that employed a plausible, biologically-motivated model to examine the independent and interdependent biomechanical and neurocomputational influences on developmental change in infant postural sway across the first year of upright walking experience. Specifically, through the implementation of an unsupervised (reinforcement-based) learning algorithm (Doya, 2000; Sutton & Barto, 1998), an autonomous model that learns through trial-and-error is

analyzed in the context of upright postural control. In addition to the learning algorithm itself, the physical model of the human body was programmed to simulate growth with the learning processes. The performance data were analyzed to relate differences between learning and incremental improvements under the two different general conditions (learning vs. learning + growth). Finally, kinematic data were recovered from the model at different points during the learning/developmental process in order to compare the model-generated sway with that observed within a longitudinal sample of human infants.

The final chapter discusses implications of the findings of this study with respect to this opening chapter. In particular, how the study findings contribute to our understanding of sensorimotor integration and its development is assessed. Of particular interest is an assessment of how an exploratory learning mechanism implemented in a growing mechanical system may lead to improved prospective control. Where applicable, references are made to related behaviors such as reaching, eye movements and locomotion in order to address developmental generalizability across the domain of 'sensorimotor behaviors'.

Chapter 2[1]

The Temporal Organization of Posture Changes During the First Year of Independent Walking

Abstract

Although the development of upright posture has received considerable attention, the quiet stance of infants in their first months of learning this fundamental behavior has not been well studied. The purpose of the present study was to characterize the time evolutionary properties, or temporal organization, of these infants' unperturbed upright stance as well as how somatosensory information influences that organization. Six healthy, full-term infants were tested monthly from walk onset until 9 months of independent walking experience while standing either independently or touching a static surface. The structure of sway was assessed through stabilogram-diffusion analysis using an exponential Ornstein-Uhlenbeck characterization. The results of this analysis revealed two new insights into postural development. First, the developmental changes in quiet stance involved a decreased rate at which sway decays to maximal variance, rather than an attenuation of the magnitude of that variance. Specifically, measures indexing amount of sway variance were significantly reduced when touching a static surface as compared with an independent stance condition, but revealed no change with increased walking experience. Further, a reduction in the average rate constant of decay indicated an increased influence of long time-scale sway corrections on the overall sway trajectory.

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[1] This chapter describes a study that was conducted under support from National Science Foundation grant #9905315 (PI: J. Clark) and has already been published. Minor changes in headings and figure/equation numbering have been made for the sake of maintaining a consistent style throughout this dissertation. The full citation is:

Metcalfe, J.S., Chen, L-C., Chang, T-Y., McDowell, K., Jeka, J.J. & Clark, J.E. (2005). The temporal organization of infant posture changes during the first year of independent stance. *Experimental Brain Research, 161*, 405-416. DOI 10.1007/s00221-004-2082-z

Second, it was shown that, at early walk ages, the use of touch both reduced the amount of variance and shifted the rate constant of sway towards longer time-scale displacements. Taken in the context of previous research, these results support the hypothesis that early postural development embodies the dual tasks of calibrating sensorimotor relations for estimation of self-motion as well as identification and tuning of control system properties.

KEYWORDS: Posture, Stabilogram, Sensorimotor, Development, Human Infant

Introduction

Approximately one month before walking onset human infants can independently maintain bipedal stance (Bayley, 1993). Over the next year, the control of both independent stance and locomotion undergo marked change (Barela et al., 1999; Clark & Phillips, 1993; Ledebt & Bril, 2000; Metcalfe & Clark, 2000; Sveistrup & Woollacott, 1996). Much of what is known about postural development during this period has been revealed with paradigms involving discrete mechanical (e.g. Forssberg & Nashner, 1982; Sveistrup & Woollacott, 1996) or sensory (e.g. Foster et al., 1996; Lee & Aronson, 1974; Stoffregen et al., 1987) perturbations. While providing valuable information regarding compensatory postural responses, studies from such paradigms offer few insights into the continuous sensorimotor control involved in sustained epochs of unperturbed stance. Characterizing the time evolutionary properties, or temporal organization, of unperturbed sway has become a critical first step towards understanding the nature of sensorimotor control in adults (Collins & De Luca, 1993; Kiemel et al., 2002; Zatsiorsky & Duarte, 2000) and thus, is an appropriate entry point for understanding sources of change in postural development (Newell, 1998). The purpose of the current study, therefore, was to

characterize changes in the temporal organization of infant posture during the first year of independent walking.

To date, there have been no empirical studies focusing on changes in the control of unperturbed independent stance during infancy. However, comparisons of toddlers (2-3 years of age) with older children and adults have indicated that postural development involves a reduction of the overall variance of sway (Newell et al., 1997; Newell, 1998; Riach & Hayes, 1987). Further, by examining the regularity of sway patterns (using a measure of approximate entropy), Newell and colleagues suggested an age-related increase in structural complexity that accompanied the decreasing sway variance (see Newell, 1998 for a review). The interpretation of these findings was that postural development involves learning to incorporate an increased number of independent degrees of freedom (e.g. body segments, joints) in the task of maintaining upright stance. A second explanation was put forth by McCollum and Leen (1989) who, using an inverted pendulum model, predicted that postural development in infants should involve a changing temporal structure that would be revealed by an increased time constant. An increased time constant reflects a reduced average rate of displacement from an upright equilibrium position and thus should also appear as a decrease in mean sway frequency. According to these investigators, and others (Adolph, 2002), developmental changes in such a mechanical characterization should result from changing anthropomorphic constraints of the infant's body (e.g. height, body proportions) as well as modifications of control strategies to incorporate a greater number of degrees of freedom to expand the permissible sway region. There have yet to be any studies of infant posture that provide empirical data to support or refute these hypothesized types of change. More important,

this knowledge gap leaves little room for understanding the nature and sources of developmental change in the sensorimotor control of posture.

Recent work on the sensorimotor control of posture in adults suggests avenues of investigation that may provide new insights into the development of upright stance. For example, adult participants who lightly (< 1 N) touch a stationary surface with their fingertip while standing quietly show a dramatic attenuation of sway variance without modifying the rate constants that describe their pattern of sway displacements (Kiemel et al., 2002). Similar results were obtained by Riley and colleagues (1997) who, using a non-rigid touch surface, found haptic influences on the magnitude of sway variance without a corresponding change in the critical time used to distinguish short versus long time-scale control regimes. According to Kiemel et al (2002), such results may be interpreted as touch enhancing sensory estimates of self-motion without modifying control parameters of the postural system such as stiffness and damping.

For infants just beginning to stand upright, however, it is questionable whether touch information is integrated with the control of quiet stance in the same manner as it is for adults. For example, a longitudinal study of the relationship between hand contact and body sway (Barela et al., 1999) revealed that the use of touch for informational purposes emerges during first months following the transition to independent locomotion. This finding suggests that walking experience facilitates the development of the ability to use touch information for estimation of self-motion. Further, in a follow up cross-sectional study of infants with 1-12 months of walking experience (Metcalfe & Clark, 2000), a reduction in sway variance was found when infants touched a static surface that afforded a limited amount of mechanical support. These investigators also revealed a concurrent

reduction in the correlation between displacements of upper and lower body segments (i.e. medial-lateral head vs. approximate center of mass movements) while touching as compared with the correlations observed during the same task performed without touch. The reduced correlations were interpreted as the infants capitalizing on the stability provided by touch to facilitate exploration of their postural coordination. However, this decreased inter-segmental coordination may also indicate an effect of touch on total body stiffness; that is, a reduction in the muscular co-contractions typically seen in newly standing infants (see also Sveistrup & Woollacott, 1996). An extension from these results is that touch may have an influence on control system parameters in addition to enhancing feedback information for estimation of self-motion. The potential for a joint influence of somatosensory information on both estimation and control processes in infants, where this has not been suggested in adults, provides an open window for investigating sources of change in postural development.

To address these issues in infants, we looked to the advances brought by the last decade of research in adult postural control, with specific reference to studies focusing on unperturbed quiet stance. In particular, Collins and De Luca (1993) developed a method known as stabilogram-diffusion analysis (SDA) that allows the characterization of the temporal organization of unperturbed stance under a variety of sensory manipulations. Using SDA, it was suggested that adult postural sway is best characterized as a stochastic process as opposed to an instance of deterministic chaos, indicating long-range correlations between past and future sway displacements (Collins & De Luca, 1994). Further, the implications of the time-evolving structure revealed through SDA, as well as other analytic techniques (e.g. Lestienne & Gurfinkel, 1988; Zatsiorsky & Duarte, 2000),

have led to over a decade of debate regarding potential control architectures for upright stance (Chow et al., 1999; Collins & De Luca, 1993; Dijkstra, 2000; Kiemel et al., 2002; Peterka, 2000). As such, the use of an approach that focuses on characterizing the temporal organization of sway provides an important first step towards the ultimate goal of understanding sources of change in postural development.

The focus of this study, therefore, was to characterize the temporal organization of infant postural sway in a quiet stance task during the first year of independent walking. Using the method of stabilogram-diffusion analysis (SDA) combined with a touch manipulation, namely, hand contact with a stationary surface, we sought to describe the time evolutionary properties of unperturbed infant sway, the influence of touch on those properties, and the nature of changes associated with increased walking experience. Specifically, this analysis was designed to test the two hypothesized types of change: whether the expected decrease in sway variance can be demonstrated during this period of early postural development and further, if the theoretical prediction of an increased time constant can be validated empirically.

Method

The data analyzed in this study were collected as part of a larger longitudinal study that was designed to fully characterize the development of sensorimotor integration in infant posture. The current analysis focuses only on characterizing the time evolutionary properties of quiet stance while the infants were standing either independently or touching a stationary surface. Thus, only the procedures relevant to this analysis are presented in detail. A summary of the full experimental protocol is provided

to describe the overall context within which the data were obtained and the remaining data and procedures are to be presented elsewhere.(Metcalfe et al., 2005b).

Participants

Six infants (3 female and 3 male; including 3 Caucasian, 1 African-American, and 2 Asian infants) were included in this analysis. All infants were healthy, full-term, and without developmental delay as validated by the Bayley Scales of Infant Development, 2nd edition (Bayley, 1993) at 6, 9, and 12 months of age. Infants entered the study when they were able to sit independently (mean age = 6.14 ± 0.86 months) and were tested monthly until they reached 9 months of independent walking experience or approximately 20 months chronological age as the mean age at walk onset was 10.97 ± 1.22 months. For the purpose of this investigation, the infant's posture was assessed only at ages when they could maintain upright stance independently; specifically from walk onset onward. Each infant's caregiver provided written informed consent prior to inclusion in the longitudinal protocol and a small payment was given to the caregiver at the end of each laboratory visit. The Institutional Review Board at the University of Maryland approved all experimental procedures for this study.

Figure 2.1. An infant standing on the small pedestal in a hands free condition. To the right is the instrumented touch apparatus. Behind the infant is the Logitech receiver and the small triangles on the infants torso are transmitters for the 6-dimensional position tracking system. The caregiver and second experimenter are excluded for simplicity of presentation.

Apparatus

The data were remotely acquired using a National Instruments A/D board (BNC-2090) and custom LabView software (National Instruments Inc.; Austin, TX). All signals were sampled at 50.33 Hz in real time and synchronized to a manual trigger at trial onset. Figure 2.1 illustrates the experimental set-up wherein each participant stood on a pedestal in a parallel stance with eyes open either independently (hands-free) or touching a stationary surface.

Touch Apparatus.. An instrumented contact surface, mounted on a support frame, was positioned to the right of each infant and at the approximate level of the iliac crest (as illustrated in Figure 2.1). This was composed of a 4.4 cm diameter convex surface that was formed by the top half of a 45.7 cm long PVC tube. The purpose of this surface was to be "touchable" without being "graspable" by the infants. The contact surface was

attached atop two support columns, each instrumented with force transducers (Interface MB-10; Scottsdale, AZ) for resolving applied hand contact forces.

Postural Sway. Center of pressure in the medial-lateral (CP_{ML}) and anterior-posterior (CP_{AP}) directions were calculated from ground reaction forces measured by a force platform (Kistler 9261A). Three-dimensional shoulder girdle and approximate center of mass displacements were sampled using a Logitech 6-dimensional position tracking system (VR Depot; Boony Doon, CA), but are not reported in this analysis.

Video. All testing sessions were displayed on a remote monitor and video taped with a standard sVHS recorder (Panasonic AG-7350) for online observation of trials during acquisition as well as later behavioral coding. The video tape records were synchronized with the analog data using an event synchronization unit (PEAK Performance Technologies; Englewood, CO) and time-stamped with a SMPTE code generator (Horita RM-50 II; Mission Veijo, CA).

Design and Procedure.

Upon entering the laboratory, the infant was provided a few minutes to become acclimated to the testing environment and experimenters. During this time, an experimenter questioned the child's caregiver about the infant's health and developmental progress. Following the acclimation period, the infant was taken to a small testing room (2.1 m × 5.5 m) that was enclosed by heavy black curtains and was introduced to a small pedestal (10 cm deep × 20 cm long × 11 cm tall) to the left of the touch apparatus and affixed to the force platform. The height of the pedestal was determined through pilot testing as sufficient to discourage infants from attempting to walk during testing, but did not interfere with their willingness to stand independently.

The infant's shoes were removed and, once placed on the pedestal, the two Logitech trackers were affixed and the position of the touch apparatus was adjusted such that the infant's arm was abducted approximately 45° and the hand was held at the approximate height of the iliac crest.

During the testing session, the infant completed 5 conditions including: independent stance (without touch), touching a stationary surface, and 3 conditions of touching a surface that was oscillating in the medial-lateral direction (frequencies = 0.1, 0.3, 0.5 Hz; amplitudes = 1.6, 0.59, and 0.36 cm, respectively). Three trials were collected in each condition and each trial lasted 60 s, with the exception of the 0.1 Hz trials, which were 90 s. The 15 trials were presented in a randomized order with the exception that the independent stance condition never occurred within the first 5 trials. This is based on previous experience with this paradigm, which has shown that infants tend not to participate in touch conditions when independent stance trials are presented first. One to three short breaks were taken between trials when needed and the total testing session lasted for 25-50 minutes depending on the infant.

This analysis focused only on the conditions in which the infants 1) stood independently and 2) touched the stationary surface. Figure 2.1 demonstrates the general task in the independent stance condition. To facilitate participation, an experimenter sat in front of the infant and attempted to maintain his or her attention with a variety of toys or books. The caregiver was always present and helped prepare the infant for each trial as well as prevent possible falls. To ensure that the infant performed the appropriate touch condition, a second experimenter was positioned to the infant's right and monitored hand contact with the touch apparatus.

Data Reduction

Behavioral coding. Following data acquisition, all trials were independently examined for valid segments of quiet posture by two trained coders. For all conditions, criteria for valid segments were: 1) standing independently from the caregiver and experimenters, 2) no dancing or bouncing movements, 3) no falling or stepping movements and 4) minimum length of 10 s. Additionally, touch had to be appropriate for the experimental condition; that is, continuously touching but not grabbing the contact surface in the touch condition and hands completely free in the independent stance condition. Small head/trunk movements (i.e. turning) and upper-limb movements (i.e. pointing) that did not disrupt the performance of the task were considered as valid postural data and were not excluded. However, any movements resulting in a disruption, such as a complete turn and lean toward the caregiver or experimenter (effectively, self-generated perturbations), were completely excluded from further analyses. Coders were instructed to record start and end times of segments to the nearest second and these times were assessed by a third experimenter. Only those segments that were in complete agreement (overlapping times) were used in subsequent analyses.

Signal Processing. Once segments of quiet stance were determined, they were extracted from the raw files using an interactive data extraction program. Prior to further analysis, the mean was removed from each segment and these data were subsequently lowpass filtered using a recursive 2nd-order Butterworth filter (f_{3db} = 5 Hz). To account for edge effects of filtering, 0.75 s (~38 samples) of data were removed from each end of all segments. As a final criterion, because the amount of time is an important variable in the computation of the parameters describing the time evolutionary properties of sway,

only the ages and conditions for which there was a minimum of 20 s of valid data after signal processing were included in further analyses. A summary of descriptive stance time variables is presented in the results section. All data extraction, signal processing and reduction were performed using custom software written in MATLAB, v. 6.0 (Mathworks, Inc; Natick, MA).

Task Measures

Vertical touch force. Mean vertical touch force (TF_V) was used as a global index of the extent to which infants were using the touch apparatus for mechanical support. Reduction of the raw touch force signal included removal of analog spikes (i.e. data points exceeding 4 within-trial standard deviations from the mean were reduced to the perimeter of that range) followed by lowpass filtering with a recursive 2nd-order Butterworth filter (f_{3db} = 5 Hz). Absolute TF_V was then calculated in units of Newtons as the mean touch force during the segment minus a baseline that was determined when the infant's hand was not on the touch apparatus in the same trial. TF_V was calculated for 60% of the static touch trials with valid postural data because some of the infants never removed their hands from the contact surface in a given trial and thus, had no valid baseline. As continuous contact was a criterion for valid segments in the touch condition, baseline data were never included in the segments analyzed for the touch condition. The values for TF_V that were subjected to statistical analysis were evenly distributed across infants and walk ages (infants $\chi^2_5 = 0.36$; walk age $\chi^2_9 = 0.29$, both $p > 0.9$).

Stance time measures. To provide general indices of standing performance, two measures of stance duration were assessed. Mean segment time (MST) was the time elapsed during a segment selected by two independent coders as quiet stance (see

Behavioral Coding above) and was chosen as a measure of how long an infant will perform a single epoch of unperturbed standing. To examine the cumulative amount of time spent standing in a given testing session, the MST's for all analyzed segments (independent stance, static touch) were summed within condition and represented as total stance time (TST). Both measures were computed in units of seconds.

Stabilogram-diffusion analysis

In the current study, we applied stabilogram-diffusion analysis (SDA) to the problem of characterizing longitudinal change in the temporal organization of infant postural sway. While a number of methods have been proposed to explore the time evolutionary properties of posture, we have chosen SDA primarily because of the short data segments that are typically obtained from infants. Specifically, because SDA relies on averaging and does not require stationary time-series, it is possible to record multiple short data segments and obtain repeatable estimates of parameters that describe the time evolutionary properties of sway.

The stabilogram-diffusion function. Stabilogram-diffusion functions (SDFs) were computed on CP_{ML} and CP_{AP} displacements for each data segment as described in previous work (Collins & De Luca, 1993; Newell et al., 1997; Riley et al., 1997). Specifically, the diffusion coefficient at a particular time-increment (d_τ) was defined as the average squared displacement between all data points (X_t) separated by the length of time τ in seconds. By computing d across a range of values of τ, one obtains a diffusion function for a single component time-series. Explicitly,

$$d_\tau = \left\langle (X_{t+\tau} - X_t)^2 \right\rangle \qquad (2.1)$$

where $\tau = 0, 0.02, \ldots, 10$ s and the values for X_t and $X_{t+\tau}$ are individual samples in the time-series of sway (the angled brackets denote averaging across all samples separated in time by τ). Thus, shown in Equation 2.1, the diffusion function represents the mean squared displacement, or variance, between current and future CP positions as a function of increasing time separation. Within both CP_{ML} and CP_{AP}, the SDFs were computed as the mean of the individual diffusion functions from each data segment. Because the length of the data segments varied due to behavioral coding, a weighting procedure was used to compute the averaged SDFs as follows:

$$\bar{d}_\tau = \frac{\sum_i d_\tau^{(i)} n_\tau^{(i)}}{\sum_i n_\tau^{(i)}} \qquad (2.2)$$

where $i = 1, 2, \ldots, m$, with m being the number of data segments. The weighting factor, $n_\tau^{(i)}$, was the number of data points used to compute the value of d_τ for the i^{th} data segment. A two-dimensional resultant (SDF_{RES}) was determined as the sum of those representing CP_{ML} and CP_{AP} displacements ($SDF_{RES} = SDF_{ML} + SDF_{AP}$). Because previous literature (Collins & De Luca, 1993) as well as preliminary analyses indicated that this resultant provides the most stable estimates, we restrict our attention only to the SDF_{RES} through the remainder of this presentation. Therefore, one infant with all conditions and testing days from walk onset to 9 months post-walking would contribute 20 SDFs for computation of the parameters describing the time evolutionary properties of their sway.

Characterizing the structure of the SDF. While computation of the SDF is straightforward, there has been considerable debate regarding the extraction of parameters that describe its shape (Chiari et al., 2000; Delignières et al., 2003; Newell et

al., 1997; Peterka, 2000; Riley et al., 1998). One of the main points of contention has been that the original characterization developed by Collins & DeLuca (1993), which involved the piecewise fitting of two discrete linear segments to the SDF, implied discontinuities in the control of stance where continuous characterizations could provide more parsimonious explanations of the observed structure (Chiari et al., 2000; Newell et al., 1997; Peterka, 2000). To date, however, the selection of a given approach has been based largely on conceptual reasons with few direct comparisons between continuous and piecewise methods. When comparisons have been made (Chiari et al., 2000; Newell et al., 1997), authors have concluded in favor of the continuous characterization.

In the current study, we chose to use a continuous characterization of the SDF. Specifically, we fit the infant SDFs with an exponential function representing time-evolving variance of the linear, first-order Ornstein-Uhlenbeck process advocated by Newell et al (1997). Our selection of this approach was based on both conceptual and empirical reasons. Conceptually, this procedure was preferred because it is derived from a continuous dynamic model[2] that explicitly accounts for both stochastic and deterministic influences on sway displacements as they unfold in time. More importantly, it provides a parsimonious means of testing the two hypothesized types of change in the development of stance control; that is, decreased variance and/or an increased time constant. Empirically, our selection was based in a comparison of both piecewise linear and exponential methods on these same data. In this comparison, we did not find strong

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[2] The first-order Ornstein-Uhlenbeck process is defined by the linear stochastic differential equation $x_t' = -kx_t + \sqrt{D}\xi_t$. The deterministic part of this model specifies a stabilizing influence on velocity (x') at each time step as an inverse proportion of current position (-kx_t). The stochastic influence is characterized by white noise (ξ_t) that is scaled by the square root of the diffusion coefficient ($\sqrt{D}\xi_t$), representing variance or noise at each time step.

qualitative or quantitative evidence for the preference of either method as a means of characterizing the shape of the SDFs and, in addition, we observed the same pattern of statistical results for touch condition and walk age (see Appendix) with both methods. With the knowledge that the pattern of results held regardless of analytic method and that both methods provided similar descriptions of the SDF, we chose to proceed with the continuous approach on the basis of interpretability.

For this characterization, an exponential function (Newell et al., 1997) of the form:

$$\bar{d}_{\tau} = \left[\frac{D}{2k}\right]\left[1 - e^{-2k\tau}\right] \qquad (2.3)$$

was fit using a Nelder-Mead direct search algorithm (function 'fminsearch.m'; Matlab, v. 6.0, Matworks, Inc.; Natick, MA). In this equation, the averaged diffusion function is predicted to increase exponentially as a function of both time interval (τ) and a rate constant denoted as *k*. This rate constant represents an average time-scale over which the sway trajectory decays towards maximal variance between present and future states and reflects similar changes as the previously discussed time constant (McCollum & Leen, 1989). That is, either an increased time constant or a decreased rate constant would reflect an increased influence of relatively long time-scale displacements on the overall structure of the time-series of sway. The diffusion coefficient, *D*, is related to the amount of noise contributing to each incremental displacement on the sway trajectory. The ratio *D/2k* is the expected value of the SDF as τ approaches infinity and, because the SDF represents the growth of variance (mean squared displacement; Equation 2.1) over increasing time intervals, *D/2k* represents the maximal variance in the time-series.

Statistical analysis

All hypothesis tests were conducted using linear mixed-model analysis of variance and covariance techniques ('Proc Mixed'; SAS, version 8.02; Cary, NC). This method was selected because it differentially accounts for fixed (e.g. experimental manipulations) and random (e.g. among- and within-subject) sources of variation as well as provides tools to control variance heterogeneity and correlated measures. This method also allows for random patterns of missing cells and thus, is well-suited for analysis of longitudinal data where missing values occur. The analysis proceeded in two general steps which involved (1) the selection of an appropriate statistical model followed by (2) the application of the selected mixed-model to linear regression.

In the first step, the initial model included Walk Age represented in monthly intervals (the interval of data acquisition), Condition (independent stance, static touch) and their interaction as class level fixed effects. Random effects were specified as Infant and the Infant × Walk Age and Infant × Condition interactions, thus controlling for among- and within-subject sources of variation. Subsequently, more complex models were assessed wherein subsets of random effects parameters as well as different covariance structures were used to account for variance heterogeneity and correlated measures amongst levels of the independent variables (Walk Age and Condition). Using a goodness-of-fit statistic, the Bayesian Information Criteria (Gagne & Dayton, 2002; Schwarz, 1978) , these various models were compared with one another and the best overall statistical model was selected for use in the regression analysis. Residuals were pooled within subject and condition when the BIC indicated that it was appropriate to do so.

With the variance-covariance structure and random effects parameters selected in the first step, a regression model was constructed to more precisely examine individual developmental change as a continuous function of Walk Age represented in days from walk onset, rather than months of data acquisition. In this step, a procedure similar to backwards selection was used to determine which fixed effects parameters (Walk Age, Condition and Walk Age × Condition) were most strongly related to the dependent variables. For all variables, 2^{nd}-order functions of Walk Age were also considered, however with the exception of one dependent variable (total stance time, see below), no 2^{nd}-order trends reached significance.

The dependent variables for this analysis included (1) measures of stance duration: mean segment time, MST and total stance time, TST, (2) measures of sway variance: the diffusion coefficient, *D* and maximal variance, *D/2k* and (3) the rate constant, *k*. For the measures of sway variance, because the residuals of prediction scaled with the range of observations, all values were transformed with a natural logarithm prior to statistical analysis. Finally, because vertical touch force (TF_V) was recorded only in the static touch condition, it was analyzed only as a function of Walk Age in days. All hypothesis tests were conducted using $\alpha = 0.05$ as the nominal level of statistical significance. Throughout the remaining presentation, main effects for Condition are presented as means ± standard errors and effects for Walk Age are discussed as regression effects (slopes ± standard errors).

Results

Task Measures

Vertical touch force. TFv was included as a global index of the extent to which the infants applied force to the contact surface for mechanical support. A regression model that included Walk Age as the only fixed effect revealed no significant change in TFv ($F_{1,25.6} = 0.06$, $p > 0.5$). Across all infants and walk ages for which TFv was computed, an average of 3.81 ± 0.23 N of downward force was applied in the static touch condition.

Table 2.1. Mean Total Stance Time in Seconds by Walk Age in Months[a]

Walk Age	M	S.E.
0	46.78	9.27
1	81.61	10.32
2	90.01	12.51
3	101.94	16.25
4	106.68	11.97
5	121.07	10.57
6	95.19	10.71
7	114.08	11.26
8	84.47	8.57
9	95.83	10.98

[a] M = mean Total Stance Time; S.E. = standard error

Stance time measures. Of the measures of quiet stance duration (mean segment time, MST; total stance time, TST), significant effects were only observed for TST. Specifically, the final regression included significant first-order ($F_{1, 50.3} = 15.81$, $p < 0.001$) and second-order ($F_{1, 46.9} = 12.66$, $p < 0.001$) terms for Walk Age, but no significant effect for Condition. With increasing Walk Age, there was a concurrent linear increase in TST at a rate of 0.67 ± 0.17 s/day.However, this rate slowed with increased

walking experience as indicated by the significant second-order term of -0.002 ± 0.001 s/day^2; resulting in a downward curvilinear trend in TST across Walk Age. Table 2.1 provides descriptive statistics for TST pooled across condition and within each level of Walk Age in months. From this table it can be seen that, with exception of the month of walk onset (walk age = 0 months), the amount of time used for computation of the SDFs ranged from 82 to 121 s with a mean of 98.99 ± 4.41 s. For MST, data segments averaged 28.37 ± 1.14 s and ranged from 12.99 to 58.12 s. By means of comparison, the amount of postural data used in previous SDA investigations has varied from 15 s trials and 45 s total stance time (Newell et al., 1997) to 90 s trials (Collins & De Luca, 1994; Collins & De Luca, 1995) and 500 s of total stance time (Chiari et al., 2000). Thus, while the difficulties inherent in studying infant postural control impose important constraints on the amount of data that can be obtained, both the MST and TST durations from this study are within the range of what has previously been used to estimate diffusion parameters.

Stabilogram-Diffusion Analysis

Exemplar SDFs along with the exponential fits are presented in Figure 2.2. These SDFs were computed on the same infant at 1-month (36 days; A,B) and 9-months (288 days; C,D) of walking age in both independent stance and static touch conditions. These exemplars have been provided as a demonstration of how the three parameters (*D*, *D/2k*, and *k*) characterize the shape of the SDF. First, one will note that the amount of variance (based on the height of the "plateau" in the SDF) in the independent stance condition (left column) is approximately twice that corresponding to the static touch condition (right column). This scaling is reflected both in the diffusion coefficient (*D*), which provides an index of the amount of variance per unit time, as well as in the maximal variance (*D/2k*)

in the infant's postural sway, both of which indicate a reduction of sway variance in the touch condition. Second, the rate constant (k) provides an index of the rate of change as the SDF decays towards maximal variance. Because of the subtlety of differences in this rate constant, the gray shaded regions have been provided for illustration. Of these four exemplars, only the SDF for the independent stance condition at 1 month (Figure 2.2a) appears to increase more sharply (more narrow gray region) than the others, reflecting an interaction between touch condition and walking experience.

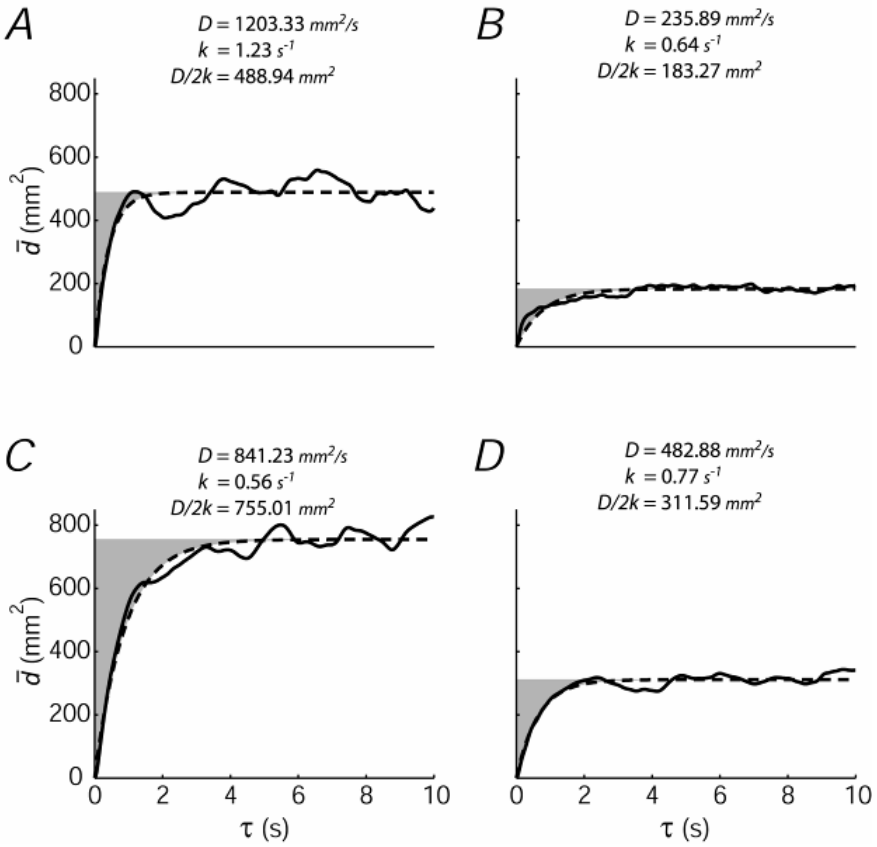

Figure 2.2: Exemplar stabilogram-diffusion functions (SDFs) computed on one infant at 1 month (A,B) and 9 months (C,D) of walking age. Independent stance condition is plotted in the left hand column and static touch is on the right. The solid line is the averaged SDF_{RES} and the dashed line is the exponential fit, both are plotted as a function of the time interval (τ) in seconds. Insets for each plot list the parameters determined through the exponential fitting procedure.

Measures of sway variance. Mixed-model regression analysis of the log-transformed diffusion coefficient (*D*), representing the amount of noise contributing to each successive sway displacement, revealed a significant effect for Condition ($F_{1, 14.3}$ = 143.59, $p < 0.001$) but not Walk Age. When the infants touched the stationary surface, the diffusion coefficient was significantly attenuated. In the independent stance condition, the untransformed mean value for *D* was 855.00 ±81.43 mm^2/s as compared with 329.25 ± 81.84 mm^2/s in the static touch condition. Similar to the diffusion coefficient, the log-transformed representation of maximal sway variance (*D/2k*) tended to decrease across Condition, but showed no trends across Walk Age. In the independent stance condition, the untransformed mean value for *D/2k* was 502.09 ± 70.70 mm^2 whereas in the static touch condition it was 418.88 ± 70.77 mm^2. However, this trend was non-significant ($F_{1, 4.97}$ = 5.68, p = 0.068).

Rate constant. For the estimated rate constant (*k*), the mixed-model regression revealed significant effects for Condition ($F_{1, 21}$ = 22.58, $p < 0.001$), Walk Age ($F_{1, 33.8}$ = 19.67, $p < 0.001$) and the Condition × Walk Age interaction ($F_{1, 24.1}$ = 6.11, $p < 0.03$). Figure 2.3 illustrates that this interaction was due to a significant decrease in the rate constant in the independent stance condition (Figure 2.3a) at -0.003 ± 0.001 s^{-1}/day ($t_{33.8}$ = -4.44, $p < 0.001$) while no change was observed in the static touch condition (Figure 2.3b). The mean rate constant in the static touch condition remained at 0.69 ± 0.11 s^{-1} across all walk ages, a value that was equivalent to that observed in the independent stance condition at 9 months of walking experience.

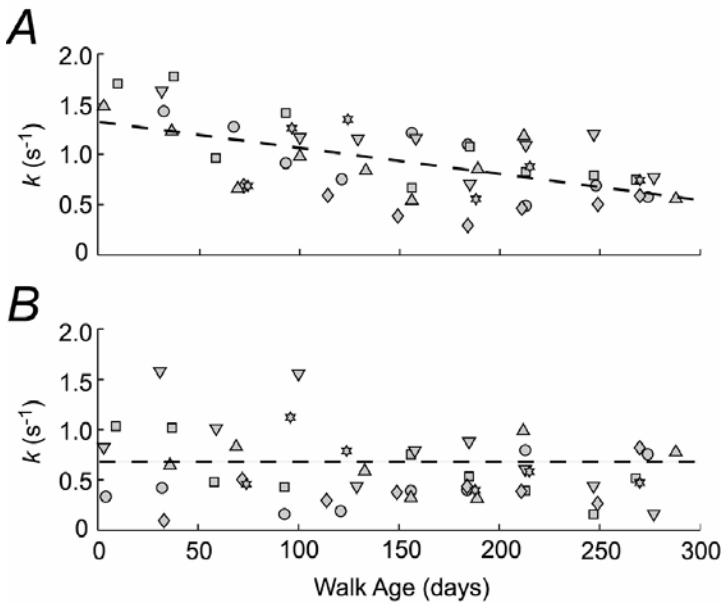

Figure 2.3. Illustration of main effects for the rate constant, *k*, in the independent stance (A) and static touch (B) conditions plotted as a function of Walk Age in days. Dashed lines indicate regression estimates from the linear mixed-model analysis. Separate markers (✡,▽,△,◇,□,○) indicate within-subject data corresponding to each individual infant.

Finally, because the estimation of the SDF can be influenced by the amount of data used and because there was a significant change in TST over the range of walk ages observed, we performed a regression analysis of k that included TST as a possible predictor variable. This analysis revealed a nearly identical pattern of results for Walk Age ($p < 0.001$), Condition ($p < 0.001$) and Walk Age × Condition ($p < 0.02$) as presented above, but provided no evidence for an influence of TST on k ($F_{1, 89.2} = 1.17$, $p > 0.2$).

Discussion

Stabilogram-diffusion analysis was used to characterize changes in the temporal organization of infant postural sway during the first year of independent walking experience. The present evidence indicated that early developmental change in continuous epochs of quiet stance involves decreasing the rate constant of sway rather

than a progressive attenuation of sway variance. Further, the use of a static contact surface led to a fundamentally different pattern of results than is typically observed in adults. That is, while in adults it has been shown that touch leads to attenuation of variance without changing rate constants, here it was shown that hand contact with a static surface influenced both the variance and average rate constant in infants. Taken in the context of previous research, these results support the hypothesis that the early acquisition and refinement of postural control embodies changes in the control system as well as calibration of sensorimotor relations for estimation of self-motion.

Sway variance: Amount vs. structure

Based on previous reports in the literature, two types of change in infant posture were expected, including reduced amount of variance and/or an increased time constant (reduced rate constant). The data examined in this study suggest that during the first year of independent walking, infants change the rate constant of their sway with no detectable change in the magnitude of variance. Specifically, a strong reduction in the rate constant was observed for the independent stance condition, indicating a slowed progression towards maximal variance between current and future postural states. In the language of Collins and De Luca (1993), this would be interpreted as increased "memory" in the postural control system with increased walking experience. Another way of discussing this, however, is to consider what a reduced rate constant means. That is, a reduced rate constant indicates a slowed initial rise of the SDF (Figure 2.2), which means that less variance is accounted for in the initial portion of the SDF where the time-scale of sway displacements is relatively short. A reduction in the rate constant thus indicates a shift towards an increased proportion of sway variance accounted for by displacements

occurring at relatively longer time-scales. This suggests that, for unperturbed independent standing, infants are learning to make less frequent postural corrections with increased walking experience.

The interesting implication of an increased influence of longer time-scale displacements comes from a robust finding in the adult literature of two major components of the postural trajectory. It has been well established that adult postural sway is well characterized on at least two time-scales including a slowly drifting mean position upon which rapid oscillations are superimposed (c.f. Collins & De Luca, 1993; Kiemel et al., 2002; Lestienne & Gurfinkel, 1988; Zatsiorsky & Duarte, 2000). The slower of these two components tends to dominate the amount of sway variance in adults and has commonly been attributed to processes involving the estimation of an internal model or a desired reference position based on the current system state (Kiemel et al., 2002; Lestienne & Gurfinkel, 1988; Zatsiorsky & Duarte, 2000). The faster oscillations around the slowly drifting mean, on the other hand, have been interpreted as corrective actions akin to a damped oscillatory feedback control process. The extension of this in reference to the current study is that early postural control may be characterized by a stronger influence of relatively rapid corrections, indicating a primacy of short time-scale feedback control. However, with increased walking experience, infants may be learning to use sensory information to more precisely estimate an internal model specifying their body position in space and thus, rely less on short time-scale feedback for the maintenance of stability; a suggestion that has been forwarded in previous studies (Barela et al., 1999; Metcalfe & Clark, 2000).

The influence of a static contact surface

The second major finding was that, unlike adults, touching a static surface influenced both the amount of variance and the rate constant of sway at younger walk ages. As already discussed, it is known that touch attenuates the sway variance of adults and infants (e.g. Jeka & Lackner, 1994; Metcalfe et al., 2005b; Metcalfe & Clark, 2000). The interpretation of this result for adults has typically been that haptic contact facilitates estimation of self-motion through enhanced somatosensory feedback (Jeka & Lackner, 1994) and, in particular, improved quality of sensory information regarding sway velocity (Kiemel et al., 2002; Oie et al., 2002). Further, studies examining the influence of touch manipulations on the temporal organization of adult sway have shown that the additional information did not change either the rate constants that described the pattern of sway displacements (Kiemel et al., 2002) or the critical time used to distinguish short versus long time-scale control regimes (Riley et al., 1997). A mechanistic interpretation of this pattern of results has been that the system control parameters, such as stiffness and damping were the determinants of the underlying rate constants of sway whereas changes in sway variance were due to enhancement of sensory estimates of self-motion.

In the current study, however, when infants with the least walking experience touched the static surface, shifts in the rate constant were observed, indicating an overlapping influence of touch and walking experience on the temporal organization of stance. Specifically, for these infants, in addition to a dramatic effect on amount of variance, touch also lengthened the amount of time (reduced rate) of decay towards maximal sway variance. The interpretation of the reduced rate constant with touch at early walking ages is that the use of the static surface led to a change consistent with

modifications in the parameters of the control system (i.e. stiffness, damping). Further support for this interpretation comes from the study of Metcalfe and Clark (2000) in which, with the use of a static contact surface, infants reduced the correlations between upper and lower body segments which might have been due to reduced overall body stiffness.

Of course, that the infants reduced their rate constant with the use of a touch surface is interesting, particularly because this does not happen with adults. However, the more difficult question is what such a pattern of results means for postural development. Previous studies have suggested that the development of posture involves a calibration or "mapping" (Bertenthal et al., 1997) of sensory information to motor action. Indeed, this is consistent with the notion that changes in sway variance with touch are due to enhancement of sensory information for estimation of self-motion. However, the quandary arises when one considers that touch has not been shown to influence the rate constants of sway in adults (Kiemel et al., 2002), but did have such an effect on the infants in the current study. These data thus call into question either (1) the hypothesis derived from the adult literature: that touch does not influence system control parameters, or (2) the hypothesis derived from the developmental literature: that ontogenetic change in postural control is restricted only to sensory "calibration" without considering the necessity of identification and tuning of the properties of the neuromuscular control system.

Because it has been shown that with walking experience infants refine the timing and sequencing of muscular activation in response to postural perturbations (Forssberg & Nashner, 1982; Sveistrup & Woollacott, 1996), modify their postural behavior in

response to altered dynamic and static sensory contexts (Barela et al., 1999; Bertenthal et al., 1997; Delorme et al., 1989; Metcalfe & Clark, 2000), and part of these changes imply improvements in estimation of self-motion (Barela et al., 1999); we suggest that it is the developmental hypothesis that should be re-considered. Explicitly, it is an incomplete explanation to assume that the development of posture is only a process of calibrating sensorimotor relations. This is because the developmental state of the effector system (e.g. growth, strength, etc) imposes constraints on the ability to form a stable internal model. It is plausible that, during early postural development, sensory information has parallel roles in identification and tuning of neuromuscular (control) system properties as well as calibration or "mapping" sensation with motor action (see Adolph, 2002; Metcalfe et al., 2005b; Metta et al., 1999 for a similar discussion).

Conclusion

Overall, the findings of this study revealed two new insights into the development of unperturbed quiet standing. First, developmental change was shown in the rate constant rather than the amount of variance, of unperturbed postural sway. Further, the reduced rate constant implied an increasing influence of long time-scale sway corrections on overall sway trajectory and is consistent with the hypothesis of a developing ability to estimate self-motion (Barela et al., 1999; Metcalfe & Clark, 2000). Second, at early walk ages, the use of the touch surface served to attenuate sway variance and, unlike adults, shift the temporal structure of sway displacements towards an increasing influence of long time-scale corrections. This replicated previous findings that relatively low-level touch forces are sufficient to attenuate sway as early as the onset of walking (Metcalfe et al., 2005b; Metcalfe & Clark, 2000) and is in part accomplished by enhancing

somatosensory estimates of self-motion. Futher, this study extends the understanding of sensorimotor contributions in that touch appears to have an additional role involving identification and tuning of system control parameters during the first year of independent walking experience.

Appendix

As there has been some controversy regarding the appropriate method for characterizing the shape of the SDF, both piecewise linear (Collins & De Luca, 1993; Riley et al., 1997) and exponential (Newell et al., 1997) methods were assessed. For this comparison, we chose to assess the two methods in three ways. First, as has been done previously (Newell et al., 1997), we performed a qualitative analysis of how well each method fit the shape of the SDF by using the proportion of variance explained (R^2). Second, to determine if differences in the R^2 were due to a differing number of parameters required to describe the shape of the SDF, we used a goodness-of-fit statistic (Bayesian Information Criteria; BIC) that explicitly penalizes more highly-parameterized models. Finally, we examined the statistical pattern of results from each method with respect to the dependent variables in this study (touch condition and walk age) to assess the sensitivity of each for detecting the effects of interest. In what follows, we first summarize how the piecewise linear (PWL) method was applied and then present the PWL results in comparison with the exponential (EXP) procedure, which was computed as described in the method section.

For the PWL method, two segments were used, providing measures of effective stochastic activity, or variance, as the half-slopes of the first (D_1) and second (D_2) portions of the linear fit. The point of inflection between the two linear regions, denoted

as critical time T_c, served as a measure of the average time constant indicating the point at which the SDF begins to plateau at maximal variance. A difference between our method and that which has previously been employed is how T_c was determined. In original applications of this technique, the linear fits were typically constrained such that T_c was found at small values of τ (< ~1.5 s). Because infant posture has not been as well characterized as adults, we developed an algorithm (described in the next paragraph) for determination of the point of inflection that considered a majority of the values of τ as possible locations of T_c.

To ensure that there were always enough data points available to fit each region of the PWL model, small portions at each end of the SDF were not considered as possible locations of T_c. The first possible point of inflection was determined by differentiating the SDF into its velocity signal and then taking the first peak. The last possible point of inflection was set at τ = 9 s, leaving 50 points for fitting the second region. Within the remaining portion of the SDF, the algorithm proceeded iteratively by computing PWL fits using each value[3] of τ as a possible inflection point. Two lines were fit on each iteration, one from 0 - τ and another from τ - 10 s, and the point where the two lines intersected served as the inflection point. Because the SDF always begins at zero (d_0 = 0), the initial intercept was fixed at zero and only the slope was estimated for the first linear segment. Both slope and intercept for the second segment were free to vary. To assess which combination of segments produced the best fit, a single line was created by concatenating the two individual lines at the inflection point and then the residual mean

[3] To reduce the computational load, the algorithm proceeded in 4 passes through progressively focused portions of the SDF. On the first pass, a relatively large step-size (SS; 20 samples) was used to find the general region around the possible inflection point (poss. infl. ± SS). On subsequent passes, SS was reduced (10, 5, 1) and the procedure was again performed using values within the smaller region of the SDF for the fitting of the two separate lines. The final value of T_c was the one determined using SS = 1.

squared error was computed against the SDF. The PWL fit with the lowest mean squared error was taken as the best piecewise representation of the SDF.

As found by Newell et al (1997), both methods explained a relatively high proportion of the variance in the SDF with little difference (~2%) between the two. For the PWL method, an overall average R^2 of 0.89 ± 0.01 (M ± S.E.) was observed as compared with 0.87 ± 0.01 for the EXP method. While these values are lower than what Newell et al (1997) reported (~0.96 – 0.98 for PWL and ~0.91 – 0.94 for the EXP), this was not unexpected given the variability inherent in shorter segments of infant postural data.

To determine whether the slightly better fits with the PWL method were due to a larger number of parameters, we also compared the two methods using the BIC. When using the BIC, the standard approach is to select the method producing the lower value. As such, we compared the two methods by subtracting the BIC values computed on the PWL fits from those computed with the EXP method ($BIC_{DIFF} = BIC_{EXP} - BIC_{PWL}$). Thus, when BIC_{DIFF} was positive, the PWL model was preferred. The mean BIC_{DIFF} was small and positive ($BIC_{DIFF} = 85 \pm 43$), suggesting that the better fits were not necessarily due to higher parameterization in the PWL method. However, a two-tail *t*-test indicated that this difference, although closely approaching significance, was marginally different from zero ($t_{95} = 1.98$, $p = 0.051$).

Finally, to assess the sensitivity of both methods for detecting the effects of interest in this study, we compared the pattern of statistical significance across analogous measures. The noise term, *D*, from the EXP method was compared with D_1 from the PWL method, since both are related to the initial slope of the SDF. The representation of

maximal variance from the EXP method (*D/2k*) was compared with the intercept of the second linear segment (D_2 int) from the PWL fit and the rate constant (*k*) was compared with the PWL critical time (T_c). For this last comparison, the reciprocal of T_c was used in order to compare the two parameters in the same units (s^{-1}). Table 2.2 summarizes the results of this comparison as discussed in the method section.

Table 2.2. Comparison of Analogous Results from Piecewise Linear and Exponential Methods

	Piecewise Linear (PWL)			Exponential (EXP)		
Effect	Measure	*F*	*p*	Measure	*F*	*p*
Condition	D_1	20.87	0.0038	*D*	143.59	<0.0001
Condition	D_2 *int*	26.50	<0.0001	*D/2k*	5.68	0.0684[a]
Condition	$1/T_c$	37.12	<0.0001	*k*	22.58	0.0001
Walk Age		14.65	0.0004		19.67	<0.0001
Interaction		9.98	0.0056		6.11	0.0209

[a] although non-significant, this value was included for comparison with the analogous PWL parameter, D_2 *int*.

Chapter 3[4]

Development of Somatosensory-Motor Integration: An Event-Related Analysis of Infant Posture in the First Year of Independent Walking

Abstract

The ability to integrate sensation with action is considered an important factor underlying the development of upright stance and locomotion. While many have studied sensory influences on posture, the nature of these influences and how they change with development has yet to be thoroughly characterized in infancy. Six infants were examined from one month prior to walk onset until 9 months of independent walking experience while standing quietly and touching either a static or dynamic surface. Five adults were examined performing an analogous task. An event-related time-frequency analysis was used to assess the relationship between postural sway and the motion of the somatosensory stimulus. Phase consistency between sway and stimulus was observed for both adults and infants and, with walking experience, the infants increased their phase consistency rather than changing aspects of response amplitude. It is concluded that walking experience provides opportunities for an active tuning of sensorimotor relations for adequate estimation of body position in space and thus, facilitates refined control over temporal aspects of postural sway.

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[4] This chapter describes a study that was conducted under support from National Science Foundation grant #9905315 (PI: J. Clark) as well as National Institutes of Health Grant #1F31 MH12963-01 (PI: K. McDowell) and has already been published. Minor changes in figure numbering have been made to maintain a consistent style throughout this dissertation. The full citation is:

Metcalfe, J.S.[†], McDowell, K. [†], Chang, T-Y., Chen, L-C., Jeka, J.J. & Clark, J.E. (2005). Development of somatosensory-motor integration: An event-related analysis of infant posture in the first year of independent walking. *Developmental Psychobiology, 46*, 19-35. DOI 10.1002/dev.20037 [[†]co-first author]

KEY WORDS: Posture, Motor, Development, Somatosensory, Sensorimotor, Integration, Event-Related, Infancy, Longitudinal, Human

Introduction

By the end of the first year of life, infants accomplish the challenging task of independent stance and locomotion. It has been proposed that the ability to integrate sensation with action may underlie this development (Barela, Jeka, & Clark, 1999; Bertenthal & Clifton, 1998; Bertenthal, Rose, & Bai, 1997). A number of investigators have addressed the issue of sensorimotor integration in the context of both adult and infant postural control. For adults, the integration of sensation with action has been robustly shown using somatosensation, vision, and multi-modal combinations of stimuli (Dijkstra, Schöner, & Gielen, 1994; Jeka, Oie, Schöner, Dijkstra, & Henson, 1998; Oie, Kiemel, & Jeka, 2002). However, the nature of this sensorimotor integration in infants, as well as how it changes with development, has not been well characterized. The majority of studies addressing sensorimotor integration in infant posture have focused on across-trial amplitude and/or average phase responses to visual cues (Barela, Godoi, Freitas, & Polastri, 2000; Bertenthal et al., 1997; Bertenthal, Boker, & Xu, 2000; Butterworth & Hicks, 1977; Delorme, Frigon, & Lagacé, 1989; Lee & Aronson, 1974). Other sensory modalities as well as other aspects of the postural response, such as within-trial amplitude and phase consistency, have been relatively neglected. To validate that postural development is dependent on adaptive sensorimotor integration, it is necessary to characterize how all relevant modalities are integrated into postural control, the response within each modality and how these relations change with development. The purpose of

the present study was to begin addressing these issues by examining the emergence of this sensorimotor relationship during the earliest period of upright stance.

Traditionally, the moving room paradigm (Lee et al., 1974; Lee & Lishman, 1975) has been a primary means of examining the linkage between posture and sensation. The general method of the moving room involves the use of dynamic manipulations of the surrounding environment to observe sensory-induced postural adjustments. For example, recent applications of this paradigm have shown that standing adults entrain their sway with small oscillations of a visual field (Dijkstra et al, 1994) or a fingertip contact surface (Jeka et al, 1998). Characteristics of the adult's response to low frequency (< 1 Hz) sensory manipulations include 1) increased sway amplitude at the frequency of the sensory stimulus and 2) a consistent phase relationship between body sway and the sensory cue, which could be interpreted in the framework of Oie et al (2002) as necessary to estimate body position relative to the environment. Stimulus frequencies in the range of ~0.2 to ~0.4 Hz typically lead to the largest amplitude and the most consistent phase responses in adults. This paradigm has been used with some success to examine sensorimotor integration in the development of posture in infancy; however, much remains to be learned about the specific nature of these responses and how they progress towards those that are so robustly observed in adults.

A few studies have examined the influence of dynamic sensory information on the postural sway of infants in bipedal standing (Delorme et al., 1989; Foster, Sveistrup, & Woollacott, 1996; Lee et al., 1974; Stoffregen, Schmuckler, & Gibson, 1987). Of these studies, only one attempted to measure infants' ability to continuously relate their body sway with an oscillating stimulus (Delorme et al., 1989). The data from this study

suggested that anterior-posterior motion of the surrounding room influenced the amplitude of the infants' anterior-posterior sway. That is, the amplitude of sway accounted for by the frequency of the stimulus was increased as compared with the surrounding frequency components. However, because frequency spectra were not reported for an appropriate control condition (static visual surround), it is difficult to attribute these results to an influence of the visual stimulus alone as opposed to a natural tendency for infants to show increased sway in the range of the stimulus frequency. Further, because the phase relationship between the stimulus and the response was not reported for either condition, this study provided no insight into the ability of infants to consistently maintain a particular phase-relationship over multiple cycles of sway behavior. Likewise, studies employing discrete movements of the visual surround have suggested developmental changes in the amplitude of sway responses such that, in new walkers, initial responses are poorly-scaled to the stimulus amplitude and often exceed biomechanical sway limits thus resulting in staggers and falls (Foster, Sveistrup, & Woollacott, 1996; Lee et al., 1974; Stoffregen, Schmuckler, & Gibson, 1987). However, the magnitude of the perturbations in these discrete tasks is more representative of a transition between two stationary environments as opposed to a dynamic relationship within a continuously changing environment. As such, it is unclear what inferences may be made from these studies regarding the *continuous* integration of sensation and postural control.

Several studies have focused on how visual information is continuously integrated with body sway during a sitting task in infants (Barela et al., 2000; Bertenthal et al., 1997; Bertenthal et al., 2000). On the whole, these studies have provided evidence for

relatively small sensory influences on sway amplitude, and only one (Barela et al, 2000) provided insight into the within-trial consistency of the phase relationship between sway and sensory stimuli. In Barela et al's (2000) study of pre-walking infants (6-9 months old), the observation of large within-trial phase variability (> 60 º) suggested that the phase relationship between the infant's sway and visual stimulus was highly variable if not completely random.

Taken together, studies of both sitting and standing 1) support influences of visual stimuli on the amplitude of postural sway in infants, and 2) hint that the temporal (phase) relationship between sway and a continuously oscillating stimulus is inconsistent prior to the onset of independent walking. These data suggest a hypothesis that the development of the amplitude and phase components of the sway response occurs differentially in ontogenetic time, a suggestion that has been made previously in studies ranging from goal-directed reaching (Konczak, Borutta, Topka, & Dichgans, 1995), visually-evoked potentials (Sokol, Zemon, & Moskowitz, 1992), vestibulo-ocular reflexes (Wiener-Vacher, Toupet, & Narcy, 1996), and interlimb coordination in walking (Clark, Whitall, & Phillips, 1988). The suggestion of differential development of amplitude and phase relations in posture is further supported by the observation of greater temporal variability in the EMG responses of young infants to a physical perturbation of the base of support than in infants with independent walking experience (Sveistrup & Woollacott, 1996). Amplitude increases without consistent phase responses suggests an extraction of relevant information from the sensory cue, but a poor estimation of body position relative to the stimulus. As such, knowledge of developmental changes in both amplitude and phase consistency are essential for a complete understanding of how infant responses

progress towards those seen in adults. Further, whether these findings hold across different sensory modalities remains unknown, but is important to assess the validity of the claim that the ability to integrate sensation with action, in all modalities, is a general factor underlying postural development.

Infant postural sway is considerably more variable than adult sway; rendering the assessment of within-trial amplitude and phase components of stimulus-response relationships a non-trivial task. To address this problem, we have adapted an event-related analysis that is based on methods used in the electroencephalographic (EEG) literature (Pfurtscheller, 1977; Sutton, Braren, Zubin, & John, 1965). This analysis relies on averaging to reveal components of a signal that are time-locked to an event (e.g., a sensory drive) but would otherwise remain hidden by a low signal-to-noise ratio. Given the variability of infant sway, the averaging process involved in an event-related analysis is well suited for assessing phase variability and interactions between amplitude and phase when examining infant postural behavior. Further, time-frequency analysis has been introduced as a way to assess non-stationary time-series across multiple cycles of observation (Kayhan, El-Jaroudi, & Chaparro, 1994) and has been suggested as an important way to examine human upright posture (Loughlin, Redfern, & Furman, 1996; Schumann, Redfern, Furman, El-Jaroudi, & Chaparro, 1995). This type of method is unique in that it can be used to study how specific components of the response unfold dynamically in time. In particular, this technique can be combined with an event-related analysis to characterize postural responses at any specific frequency such as that of the driving stimulus. By using the event-related method alone, or in combination with the time-frequency analysis, we can ask particular questions regarding the nature of the

developing sensorimotor relationship. For example, do infants who increase their response amplitude to both discrete and continuous stimuli prior to independent walking stabilize the temporal relationship between themselves and the environment with increasing upright experience? If this were true, it would support the hypothesis that the development of the ability to estimate body position relative to the environment, rather than the more general ability to integrate sensation with action, underlies the development of independent upright stance and locomotion.

In this paper, our first aim is to provide convincing evidence of infants' abilities to integrate haptic cues with postural sway. To accomplish this, we compare infant and adult postural responses to somatosensory cues in order to confirm the efficacy of our selected event-related time-frequency analysis technique. That is, the validity of the method could be questioned if it lacked the power to detect differences between the consistent responses of adults as compared with those of infants. The results of this comparison, if positive, would enable the pursuit of our primary purpose; to examine the longitudinal pattern of change in postural responses to somatosensory cues as infants gain experience in the upright. Relative to this primary purpose, our hypothesis is that from walk onset onwards, development of the stimulus-sway relationship will be characterized by increasing temporal consistency as opposed to changes in stimulus-related sway amplitude.

Method

Participants

Six infants (3 female; 3 male), who were part of a larger longitudinal study, were included in this analysis. All infants were healthy, full-term, and without developmental

delay as assessed by the Bayley Scales of Infant Development, 2nd edition (Bayley, 1993). Infants entered the study when they were able to sit independently (mean age = 6.14 ± 0.86 months) and were tested monthly until they reached 9 months of independent walking experience (mean age at walk onset = 10.97 ± 1.22 months). For the purpose of this investigation, infants were assessed only at ages when they could maintain upright stance while using single-hand support; specifically from 1 month prior to walk onset onward. Each infant's parent or guardian provided written informed consent prior to inclusion in the longitudinal protocol and a small payment was given to the parent or guardian for each laboratory visit. To provide a control group for comparison, five healthy adults (2 female; 3 male) were also included in the analysis. The five adults (mean age = 29.8 ± 8.2 years) were unpaid volunteers who provided written informed consent. The Institutional Review Board at the University of Maryland approved all experimental procedures for this study.

Apparatus

All data were remotely acquired with a Windows NT workstation (Intergraph TDZ-2000) using a National Instruments A/D board (BNC-2090) and custom LabView software. All signals were sampled at 50.33 Hz, in real time, and synchronized to a manual trigger at trial onset. Figure 3.1 illustrates the experimental set up for infants, wherein each participant stood on a pedestal mounted on a force platform in parallel stance with eyes open and with the hand touching a dynamic (oscillatory) or static surface; adults stood on a pedestal in an analogous position.

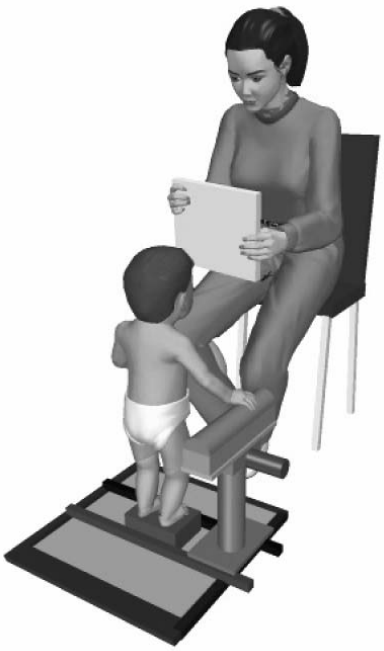


Figure 3.1. An infant standing on the small pedestal in a static touch condition. The experimenter maintained the infant's attention with a variety of books or toys. Omitted are the infant's parent or guardian who sat close enough to prevent the infant falling, the second experimenter who monitored the infants hand contact with the touch apparatus, and the Logitech tracking system (see text).

Touch Apparatus. For the infants, an instrumented touch bar, mounted on a support frame, was positioned to the right of each participant and aligned with the top of the iliac crest. The touch bar was composed of a 4.4 cm diameter convex surface, formed by the top half of a 45.7 cm long PVC tube. The purpose of this convex surface was to be "touchable" without being "graspable" by the infants. The contact surface was attached atop two support columns, each instrumented with force transducers (Interface MB-10) for resolving applied hand contact forces. Vertical touch forces were recorded with negative values indicating downward application of force. The entire touch bar was mounted on a precision linear positioning table (Daedal 105002BT) and driven by DC brushless motor (Compumotor SM231AE) controlled by a torque servo drive (Compumotor OEM675T). For the adults, the contact surface was a circular metal plate 5

cm in diameter mounted on a tripod and positioned to the right and forward of each participant at approximately hip level. Both the touch apparatus and servo control system for the adults were identical to those described in previous reports (Jeka et al., 1998; Oie et al., 2002).

For all participants, the servomotor was experimentally controlled by specifying movement amplitude as well as peak velocity and acceleration. Touch surface position was measured using a precision optical encoder attached to the end of the servomotor. The encoder produced 1000 pulses per revolution and a custom circuit monitored the motor's direction and counted the number of encoder pulses to enable D/A conversion at a resolution of 0.004 mm. To account for the inertial properties of the different contact surface sizes, both servo controllers were tuned such that resulting motion profiles were equivalent.

Postural Sway. Center of pressure in the medial-lateral (CP_{ML}) and anterior-posterior (CP_{AP}) directions were calculated from ground reaction forces measured by a force platform (Kistler 9261A). Three-dimensional shoulder girdle and approximate center of mass displacements were also sampled using a Logitech 6-dimensional position tracking system (VR Depot; Boony Doon, CA), but are not reported in this analysis.

Videotaping. All infant testing sessions were displayed on a remote monitor and videotaped with a standard sVHS recorder (Panasonic AG-7350) for online observation of trials during acquisition as well as later behavioral coding. The videotape records were synchronized with the analog data using an event synchronization unit (PEAK Performance Technologies) and time-stamped with a SMPTE code generator (Horita RM-50 II).

Design and procedure

The data for this paper are from a larger longitudinal study designed to examine quiet stance as well as the use of somatosensory information in the development of posture. Here we describe in detail the procedures relevant to our questions and only a summary of the full experimental protocol is provided to illustrate the context within which these data were obtained. The remaining data and procedures are to be presented elsewhere (c.f. Metcalfe et al., in press).

Infants. Upon entering the laboratory each month, the infant was provided a few minutes to acclimate to the testing environment. During this time, an experimenter questioned the parent or guardian about the infant's general health and developmental progress during the previous month. Following the acclimation period, the infant was taken to a small testing room (2.1 m × 5.5 m) that was enclosed by heavy black curtains and was introduced to a small pedestal (10 cm deep × 20 cm long × 11 cm tall) placed to the left of the infant touch bar and affixed to the force platform. The infant's shoes were removed and, once placed on the pedestal, the two Logitech trackers were affixed and the position of the touch apparatus was adjusted such that the infant's arm was abducted approximately 45° and the hand was aligned with the top of the iliac crest.

Figure 3.1 provides a simplified illustration of the postural task for an infant in the touch condition. To facilitate participation, an experimenter was positioned in front of the infant to best maintain the infant's visual attention on one of a variety of toys or books. The parent or guardian was always present and helped position the infant for each trial as well as prevent any possible falls. To ensure that the child performed the appropriate

touch condition, a second experimenter was positioned to the infant's right side and monitored hand contact with the touch bar.

During the testing session the infant completed 5 conditions including: independent stance (without touch), touching a static surface, and 3 dynamic conditions of touching an oscillating surface (frequencies = 0.1, 0.3, and 0.5 Hz; amplitudes = 1.6, 0.59, and 0.36 cm, respectively). Three trials were collected in each condition and all trials lasted 60 s, with the exception of the 0.1 Hz trials, which were 90 s. The 15 trials were presented in randomized order. An exception to the random presentation was that an independent stance ('no touch') trial never occurred within the first 5 trials. This is based on previous experience with this paradigm which has shown that infants tend not to participate in touch conditions when independent stance trials are presented first. Following completion of all experimental conditions, the infant's height and weight were recorded for future reference.

Adults. Upon entering the laboratory the experimental procedures were explained to the participant and the informed consent form was provided for reading. After signing the consent form, the adult removed his or her shoes and was taken to a small testing room (2.1 m × 5.5 m), which was enclosed by heavy black curtains. Within the testing room, the two Logitech trackers were affixed, and the participant stood on a block (19 cm deep × 40.5 cm long ×29.5 cm tall) that was centered on the force platform and placed to the left and behind the adult touch plate. The purpose of this block was to create a pedestal analogous to that used for the infants, but scaled to the adult's larger body size. Therefore, the positioning of the adults' feet on the pedestal as well as the location of the touch plate approximated the posture of the infants. Similar to Figure 3.1, the postural

task analyzed in this study required the participant to stand quietly on the pedestal while touching the contact surface and maintaining visual attention on an object positioned at eye height. Following completion of all experimental conditions, the participant's height and weight were recorded for future reference.

During the testing session, the adult participant completed 4 conditions including: independent stance (without touch), touching a static surface, touching an oscillating surface similar to the infants (frequency = 0.3 Hz; amplitude = 0.59 cm), and touching an oscillating surface in which the amplitude of oscillation at 30 s was reduced in half (to an amplitude of 0.3 cm) and then subsequently stopped oscillating for the last 30 s of the trial (60 – 90 s). Two trials were collected in each condition and all trials lasted for 30 s with the exception of the decreasing-amplitude trials, which were 90 s. The 8 trials were presented in a randomized order.

For the purposes of this report, our analyses focused only on the conditions in which the infants and adults 1) touched a static surface and 2) touched a dynamic surface (0.3 Hz oscillation). To examine the postural relationship with the stimulus, we specifically analyzed the response to the 0.3 Hz frequency because 1) it is in the range of frequencies in which adult sway responses typically show the largest amplitude and most consistent phase and 2) the period of oscillation at 0.3 Hz is short enough (3.33 s) that the infants in this study could perform the task over multiple cycles of stimulus oscillation within a given data segment (minimum = 15 s, ~5 cycles; see below). The data from the remaining conditions are beyond the scope of this investigation and will be the subject of a future report on frequency response characteristics of infant sensorimotor integration.

Data reduction

Behavioral coding. Because infants rarely stand quietly for the entire duration of a trial, the data analysis was based on individual segments of quiet stance within the completed trials. As such, following data acquisition, all infant trials were independently examined

Table 3.1. Summary of the Average Amount of Data Contributed at each Walk Age

Walk Age (months)	Walk Age (days)	*n*	Amount of Data (sec)
-1	-20.40 *(6.07)*	4	66.25 *(41.06)*
0	4.33 *(3.08)*	5	33.33 *(18.22)*
1	33.50 *(2.43)*	5	59.33 *(22.53)*
2	66.43 *(6.08)*	6	55.28 *(30.97)*
3	96.40 *(3.51)*	5	58.67 *(29.66)*
4	123.83 *(6.62)*	6	98.06 *(68.27)*
5	155.00 *(3.46)*	5	73.67 *(37.87)*
6	185.83 *(2.14)*	6	60.83 *(32.74)*
7	212.83 *(1.33)*	5	59.44 *(29.96)*
8	247.75 *0.96*	3	43.89 *(22.99)*
9	274.50 *(7.37)*	6	49.44 *(24.26)*

Notes: n = number of infants contributing data at each walk age; standard deviations are reported in parenthesis under each mean.

for valid segments of quiet posture by two trained coders[5]. Criteria for valid data segments were: (1) minimum length of 22 s (15 s plus edges, see below), (2) continuously touching, but not grasping the contact surface, (3) standing independently without assistance of the experimenter or caregiver, (4) no dancing or bouncing movements and (5) no falling or stepping movements. Small head/trunk movements (i.e. turning) and upper-limb movements (i.e. pointing) that did not disrupt the maintenance of stance were considered as valid postural data and were not excluded. However, any movements resulting in a disruption of the task, such as a complete turn and lean toward the parent/guardian, were completely excluded from further analyses. Coders were instructed to record start and end times of segments to the nearest second and these times were assessed by a third experimenter. Only those data segments that were in complete agreement (overlapping times) were taken as reliable data[6]. Once the segments of quiet stance were determined, they were extracted from the raw files using an interactive data extraction program. Table 3.1 presents a summary of the average and standard deviation of the amount of data contributed after behavioral coding at each level of walk age. Adult data were not coded, as these participants were able to complete the task in the specified duration without actions that invalidated trial segments.

Signal Processing. All data extraction, reduction and signal processing were performed using custom software written in MATLAB (Mathworks, Inc; Natick, MA).

[5]Coders underwent an extended training protocol involving (1) explanation and definition of the behavior of interest; i.e. quiet posture, (2) explanation of our behavioral coding scheme, (3) test coding of a subset of trials that had already been successfully and reliably coded by the lead experimenters, and (4) assessment of the trainee's agreement with the established procedure. A coder was not allowed to assess data to be analyzed until their coding was in agreement with segments selected by the established procedure.

[6] Inter-rater reliability was set at 100% by definition. It was never the case that disagreement between coders occurred across trials. If a segment of quiet stance was found within a given trial, it was noted by both coders and only the portions of time where both coders were in agreement were used for further analysis.

To address specific aspects of the data, several analyses were conducted. Analyses were performed using two filtering parameters. For the first analysis, hereafter referred to as *total sway*, a recursive low-pass filter (2nd order Butterworth; f_{3db} = 5 Hz) was applied to the raw data following removal of the mean. To specifically examine the influence of the 0.3 Hz drive on sway, the second analysis, hereafter referred to as *0.3 Hz sway*, used a time-frequency methodology. This time-frequency method used a recursive band-pass filter in a narrow range around the driving frequency of the stimulus (0.3 Hz) and is a similar to techniques used in studies of EEG (Pfurtscheller, 1977). Specifically the raw data, with the mean removed, were band-pass filtered (f_{3db} = 0.2, 0.4 Hz) using a 2nd order Butterworth filter (see Figure 3.2b; raw data in Figure 3.2a). Of the number of time-frequency analysis techniques available, each suffers some limitation (Kayhan et al., 1994; Schumann et al., 1995). Our results will validate that the method chosen here was well-suited to examine the questions posed in this study. Based on the characteristics of both filters, 3.5 s were uniformly removed from either end of all filtered data to account for edge effects[7].

Sway Amplitude. The first measures generated from this analysis were amplitude variables, which were computed irrespective of stimulus motion. Amplitude (AMP) was the RMS of the filtered data and was calculated for total and 0.3 Hz sway. For total sway, AMP is equivalent to mean sway amplitude (the standard deviation of the total time-series). For 0.3 Hz sway, AMP is analogous to the spectral amplitude of the 0.3 Hz sway

[7] Because filtering involves fitting polynomials to time-series, some distortion always appears as transients at the extremes of the data series due to small number of samples (e.g. "edge effects"). This has also been discussed as the "end point problem" (Phillips & Roberts, 1983). The extent of the edge effects for these filters was estimated by comparing pre- and post-filtered idealized waveforms (sine waves) of different frequencies. The maximum transient length observed was 3.5 s and thus was chosen as a uniform amount of time to be removed from all post-filtered data.

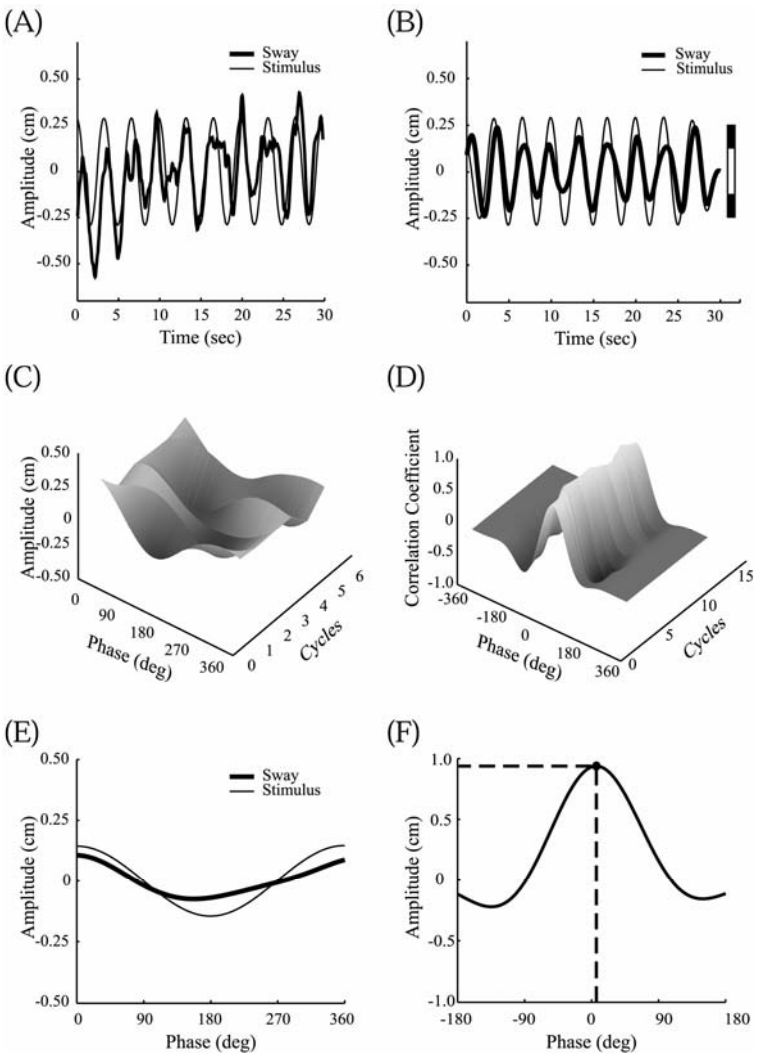


Figure 3.2. Exemplar of the methodology applied in the dynamic condition for a healthy adult. (A) Raw time-series of postural sway (heavy line) and the stimulus (thin line). (B) Data from A bandpass filtered with a passband from 0.2 to 0.4Hz, thus yielding the 0.3Hz sway. Note the attenuation of the signals at each end; these edge effects were removed from all filtered data (see Signal Processing). The solid white bar at the end of the time-series indicates the computed AMP, with the black bars on the top and bottom indicating AMP_{VAR}. (C) Sway amplitude and (D) sway-stimulus cross-correlations plotted across phase for each stimulus cycle. (E) Sway amplitude from C averaged across time-locked cycles; the RMS of this averaged signal yields AMP_{TL}. (F) The cross-correlation functions from D averaged across time-locked cycles; horizontal dashed line indicates CC_{TL} and the vertical dashed line indicates LAG_{TL}. These same steps were also applied to the total sway (lowpass filtered at 5 Hz cutoff), see Method for details.

component (e.g. the amplitude spectrum obtained using the Fourier transform) and thus,

is related to the amount of sway amplitude accounted for at 0.3 Hz (see Figure 3.2b,

white side-bar). Amplitude variability (AMP_{VAR}; Figure 3.2b, black side-bars) was determined as the standard deviation of the AMP that was computed for both total and 0.3 Hz sway. Because AMP and AMP_{VAR} are computed on the sway irrespective of the behavior of the stimulus, they yield only indirect measures of the influence of the dynamic stimulus on postural sway.

Event-Related Measures. To examine the relationship of sway and stimulus directly, an event-related technique was used to assess average phase, phase variability, and the potential interactions between amplitude and phase. A summary of all dependent measures from this event-related time-frequency analysis is presented in Table 3.2. For the dynamic condition, sections of sway data were time-locked to the repeating cycles of stimulus motion, treating the beginning of each cycle as the event. For the static condition, time-locked measures were computed relative to a simulated stimulus. The purpose of using this simulated stimulus was to provide a basis of comparison between the static and dynamic conditions. The simulated stimulus was created as a zero-phase 0.3 Hz sinusoid that was scaled to the amplitude of the actual 0.3 Hz stimulus from the dynamic condition. Because this stimulus did not exist for the static touch condition, that is the contact surface was actually stationary, measures computed on it served as an indication of how they should behave when the stimulus and response are independent of one another (i.e. creating the null hypothesis; any measure computed relative to the simulated stimulus in the static touch condition should represent an arbitrary relationship). Using these stimuli (real and simulated), several time-locked measures of amplitude and phase were then computed for both conditions as described in the following paragraphs.

Table 3.2. Summary of Event-Related/Time-Frequency Dependent Variables

Frequency Component	Dependent Variable	Computation	Represents
Total Sway (lowpass filtered; 5 Hz cutoff)	AMP	RMS of lowpass filtered time-series irrespective of stimulus oscillation.	The average displacement from upright equilibrium; analogous to mean sway amplitude.
	AMP_{VAR}	Standard deviation of AMP computed on the lowpass filtered time-series.	The variance of the mean displacement from upright equilibrium; measures within-trial consistency of sway amplitude.
	AMP_{TL}	RMS of the filtered time-series after time-locking to repeated cycles of stimulus oscillation (360° intervals).	The cycle-by-cycle consistency of both amplitude and timing (phase) of the overall sway response to the stimulus.
	CC_{TL}	Maximum of the averaged cross-correlation functions across time-locked ½ stimulus cycles (180° intervals).	The cycle-by-cycle consistency of the relationship between the overall sway response and the stimulus; sensitive to both magnitude and time lag of the correlation function.
	LAG_{TL}	Value of the time-lag associated with the maximum CC_{TL}	The average time-difference between stimulus motion and the overall sway response across repeated cycles of stimulus oscillation.
0.3 Hz Sway (bandpass filtered; 0.2, 0.4 Hz cutoff)	AMP	RMS of bandpass filtered time-series irrespective of stimulus oscillation.	The average amplitude of the sway occurring at 0.3 Hz; analogous to the spectral amplitude determined using a Fourier transform.
	AMP_{VAR}	Standard deviation of AMP computed on the bandpass filtered time-series.	The variance of the amplitude of sway occurring at 0.3 Hz; measures within-trial consistency of the sway occurring at the driving frequency.
	AMP_{TL}	RMS of the 0.3 Hz time-series after time-locking to repeated cycles of stimulus oscillation (360° intervals).	The cycle-by-cycle consistency of both amplitude and timing (phase) of the 0.3 Hz sway component.
	CC_{TL}	Maximum of the averaged 0.3 Hz cross-correlation functions across time-locked ½ stimulus cycles (180° intervals).	The cycle-by-cycle consistency of the temporal relationship between the 0.3Hz sway component and the stimulus; similar to coherence (shared power) between stimulus and response at 0.3 Hz.
	LAG_{TL}	Value of the time-lag associated with the maximum 0.3Hz CC_{TL}	The average time-difference between stimulus motion and the 0.3 Hz sway component; analogous to the average relative phase between the stimulus and 0.3 Hz sway component.

Time-locked amplitude (AMP_{TL}) was computed by windowing the filtered data to a length equal to one cycle of the stimulus (sampling rate/drive frequency; 50.33/0.3, ~ 168 samples) with no overlap (i.e., cycles were locked at 360° intervals throughout the data segment). The time-locked sections of data (Figure 3.2c) were then averaged across individual cycles of the stimulus (Figure 3.2e). AMP_{TL} was then determined by computing the RMS of the averaged signal across time-locked cycles, reflecting an interaction between the amplitude and phase of the sway response.

Time-locked cross-correlations (CC_{TL}) were used to index the phase as well as cycle-by-cycle phase variability between the signal and the sway response. Similar to AMP_{TL}, CC_{TL} between the filtered sway and the stimulus signals (signals shown in Figure 3.2a-b; correlation functions in Figure 3.2d) were computed for each cycle. The correlation functions were calculated using 10% Hanning windows with a 50% overlap (i.e., cycles were locked at 180° intervals throughout the data segment). The correlation functions were then bias-corrected and averaged across cycles. CC_{TL} was defined as the absolute maximum of the averaged correlation function (Figure 3.2f, horizontal dashed line) and time-locked lag (LAG_{TL}) was the time at which the maximum positive correlation was found (Figure 3.2f, vertical dashed line). In both dynamic and static conditions, because of the narrow band-pass filter at 0.3 Hz, individual cycle correlations with the 0.3 Hz stimulus will always reach a maximum of 1.0. Thus, the 0.3 Hz sway CC_{TL} reflects only the variability of the phase of the postural signal; that is, if the phase is stable from cycle to cycle, CC_{TL} will approach a value of 1 whereas if the phase varies from cycle to cycle, CC_{TL} will be reduced. For total sway, CC_{TL} reflects both the variability of the phase of the postural signal as well as the magnitude of the correlation

between the sway and the stimulus. In both cases, LAG_{TL} is analogous to the average phase.

Infant touch forces. Mean vertical touch force (TF_V) was used as a global index of the extent to which infants were using the touch apparatus for mechanical support. Reduction of the raw touch force signal included removal of analog spikes (i.e. data points exceeding 4 within-trial standard deviations from the mean were reduced to the perimeter of that range) followed by lowpass filtering with a recursive 2nd order Butterworth filter (f_{3db} = 5 Hz). Absolute TF_V was then calculated as the mean touch force during the data segment minus a baseline that was determined by the transducer output when the infants hand was not on the touch apparatus in the same trial. TF_V was calculated for 58% of the trials with valid postural data because some of the infants never removed their hands from the touch bar in a given trial and thus, had no valid baseline. As continuous hand contact was a criterion for valid segments in the touch conditions, baseline data were never included in the touch data. The values of TF_V that were tested statistically were evenly distributed across infants, conditions and walk ages (infants χ^2_5 = 0.35; conditions χ^2_1 = 0.001; walk ages χ^2_9 = 0.57, all $p > 0.9$).

Statistical analysis.

The analysis procedure for this experiment was performed in two steps. In the first step, univariate repeated-measures ANOVAs were used to provide convincing evidence of infants' abilities to integrate haptic cues with postural sway through a comparison of the postural responses of infants and adults. The 2 × 2 ANOVAs contained one between-subjects factor, Age (infant, adult), and one within-subjects factor, Condition (static, dynamic) and were performed to examine AMP, AMP_{VAR}, AMP_{TL}, and

CC_{TL} for total and 0.3 Hz sway in both medial-lateral and anterior-posterior sway directions. Because the simulated stimulus used in the static condition was at an arbitrary phase relative to the sway, LAG_{TL} had no meaning for the static condition. As such LAG_{TL} from the dynamic condition was tested using one-way ANOVAs with Age (infant, adult) as a between subjects factor.

While the first step of the analysis addressed the issue of detecting a postural response to the stimulus and discriminating differential effects based on age group, the second step was designed to examine longitudinal changes in the sway response of infants. For this purpose, linear mixed-model regression (SAS, version 8.02; Cary, NC) was used to examine all dependent variables for the influence of Condition (static, dynamic) and Walk Age. Walk age was used to normalize all data to the individual infant's developmental level and was computed as both months and days elapsed from walk onset. Walk onset was defined as the age at which the infant first took three independent steps.

The mixed-model analysis was chosen because it separately controls fixed (i.e. Condition) and random (i.e. Infant) sources of variation as well as provides tools to account for variance heterogeneity and correlated measures. For this analysis, class level fixed effect variables were specified as Condition (dummy variable; 0 = static, 1 = dynamic) and Walk Age in months of data acquisition (integer intervals). Random effects were specified as due to Infant as well as the Infant × Condition and Infant × Walk Age interactions. Residuals were blocked within infant and stimulus condition and the variance-covariance matrix was structured with a first-order autoregressive function. This structure was selected to account for correlations between subsequent intervals of Walk

Age with the assumption that ages that are closer together (e.g. 1- and 2-months) display a higher correlation than those that are separated by a larger time intervals (e.g. 1- and 9-months). With above parameterization, the mixed-model was applied to a linear regression across Condition, Walk Age in days and the Condition × Walk Age interaction. Values for LAG_{TL} were again examined only in the dynamic condition and thus, simply regressed across Walk Age.

For both steps in the analysis, hypothesis tests were conducted on weighted averages within each individual and condition, using the amount of data obtained (e.g. number of cycles) as the weighting factor. Further, correlation coefficients were normalized using a Fisher's Z transformation and the amplitude variables (AMP, AMP_{VAR}, AMP_{TL}) were normalized using the natural logarithm prior to hypothesis tests. For clarity, variables are reported in their un-transformed metric in all plots and descriptive statistics. All effects were tested at a significance level of $\alpha = 0.05$. Finally, with the exception of age-related variables, which are shown as means ± standard deviations, all effects are represented with means and standard errors.

Results

Exemplar sway responses for both adults and infants are illustrated in Figure 3.3 for the dynamic condition (0.3 Hz stimulus). Two-dimensional plots of low-pass filtered (Figures 3.3a-b) and band-pass filtered (Figures 3.3c-d) sway trajectories reveal important aspects of the postural response. First, the total sway of the adult (Figure 3.3a) showed dramatically reduced amplitude compared to that of an infant performing an

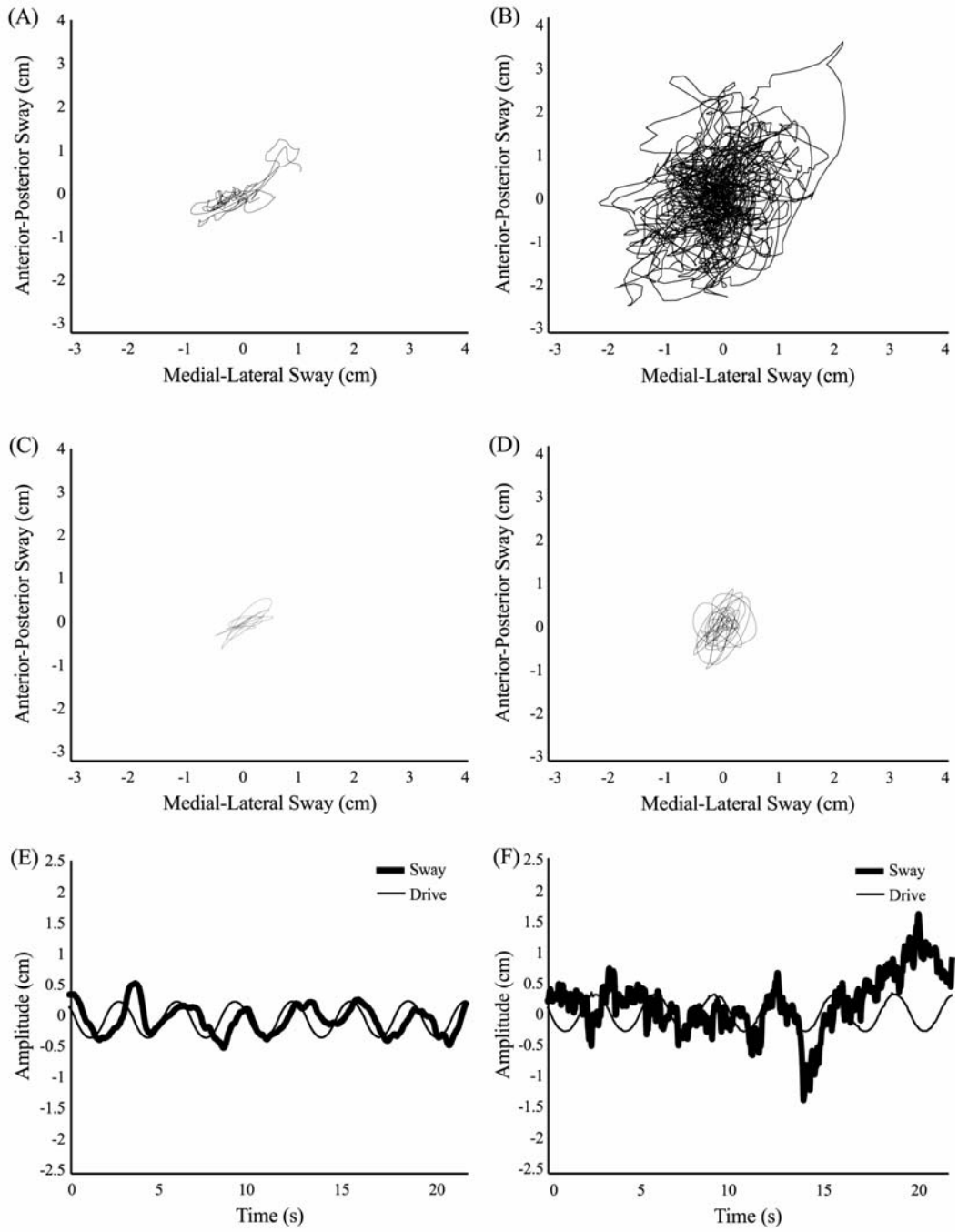


Figure 3.3. Exemplars of adult and infant center of pressure sway responses in the dynamic condition (0.3Hz stimulus). Two-dimensional stabilograms of the low-pass filtered sway response are illustrated for (A) an adult and (B) an infant with 6-months of walking experience. Likewise, the 0.3 Hz sway component are shown for (C) the adult and (D) the infant. In adults (E), a close relationship is observed between the low-pass filtered time-series of medial-lateral sway (heavy line) and the stimulus (thin line). In infants (F), the relationship between low-pass filtered time-series of medial-lateral sway (heavy line) and the stimulus (thin line) is difficult to observe.

analogous task (Figure 3.3b). Second, when the 0.3 Hz component was extracted for the adult sway (Figure 3.3c), the amplitude of the 0.3 Hz sway appeared similar to the amplitude of the total sway response. In contrast, the infant's 0.3 Hz component was proportionally a smaller component of the total sway (Figure 3.3d).

Further, in all trajectories, one can see that the response to the medial-lateral stimulus was not confined only to the medial-lateral direction. In both total sway and 0.3 Hz sway, the postural trajectories appeared oriented in a resultant direction, intermediate to the anterior-posterior and medial-lateral axes. Finally, the exemplars of the medial-lateral sway component (Figures 3.3e-f) highlight the importance of the analysis technique employed in this study. While the adults sway demonstrated a relatively strong influence of the stimulus (Figure 3.3e), which could be analyzed with standard techniques (Dijkstra et al., 1994), the infants response to the dynamic stimulus was much less apparent and masked by large variability (Figure 3.3f). The data in these figures illustrates the reason why alternative analysis techniques discussed in the method section above were considered appropriate for understanding infant postural control.

Infants vs. Adult Controls

The first step of the analysis attempted to provide convincing evidence of infants' abilities to integrate haptic cues with postural sway as well as to verify that the methods used herein had the power to detect stimulus influences on the sway of the infants. For this analysis, all infants (n = 6) at 6 months post-walking (M = 185.83 ± 2.14 days of walking experience) were compared with the adult controls using univariate 2 (Age: infant, adult) × 2 (Condition: static, dynamic) repeated-measures ANOVAs for all

variables except LAG_{TL}, which was examined only for Age effects in the dynamic condition. All significant results for this comparison have been summarized in Table 3.3.

Table 3.3. Summary of Infant versus Adult Results

		Medial-Lateral Sway			Anterior-Posterior Sway		
		Age	Cond.	Age x Cond.	Age	Cond.	Age x Cond.
Total Sway	AMP	**	-	-	**	-	-
	AMP_{VAR}	**	-	-	**	-	-
	AMP_{TL}	-	*	-	-	-	-
	CC_{TL}	**	**	-	*	*	-
0.3 Hz Sway	AMP	**	-	-	*	-	-
	AMP_{VAR}	**	-	-	*	-	-
	AMP_{TL}	-	*	-	-	**	-
	CC_{TL}	**	**	*	*	**	-

Notes: * = $p < .05$; ** = $p < .01$; LAG_{TL} results are not summarized as a different statistical design was performed on this measure and no significant results were observed.

Total Sway. To examine the differential effects of the dynamic stimulus on the total sway response of the infants and adult controls, 2 × 2 ANOVAs were applied to all measures computed on the low-pass filtered data. In this analysis, effects of Condition were revealed for CC_{TL}, which was computed in relation to the stimulus in the dynamic condition but versus an identical, but simulated, stimulus in the static condition. As can be seen in Figure 3.4a, CC_{TL} was significantly increased in the dynamic stimulus condition for both medial-lateral ($F_{1,9} = 24.59$, $p < 0.01$) and anterior-posterior ($F_{1,9} = 7.29$, $p < 0.05$) sway. The only amplitude measure that revealed a main effect for Condition was AMP_{TL} in the medial-lateral direction ($F_{1,9} = 5.52$, $p < 0.05$). For the static

condition, AMP_{TL} was reduced (0.14 ± 0.02 cm; *M* ± *S.E.*) as compared with that observed in the dynamic condition (0.21 ± 0.04 cm).

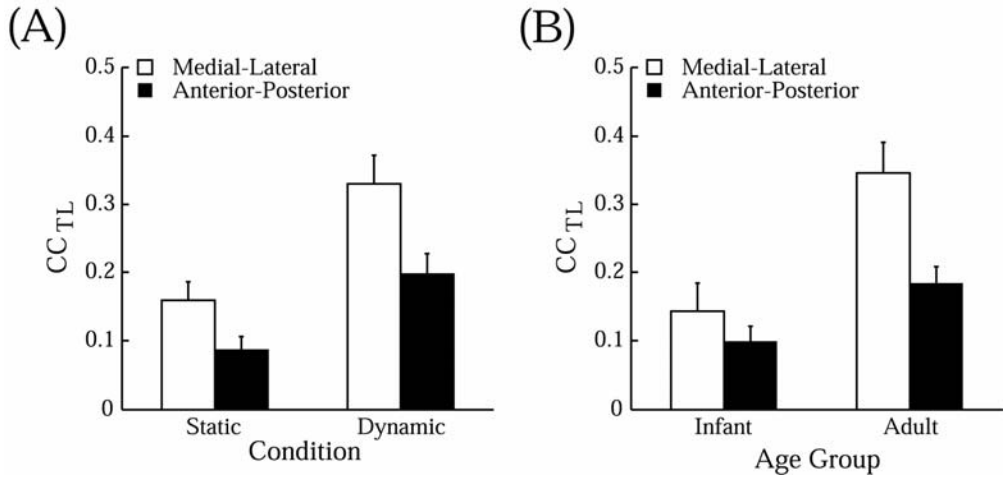


Figure 3.4. Time-locked cross-correlations (CC_{TL}) computed on total sway. Main effects for (A) Condition and (B) Age for medial-lateral (white bars) and anterior-posterior sway (dark bars). Bars represent *M* ± *S.E.*

Age main effects were observed in the measures of AMP, AMP_{VAR}, and CC_{TL}. For adults, CC_{TL} was greater than for infants in both the medial-lateral ($F_{1,9} = 10.59$, $p < 0.01$) and anterior-posterior ($F_{1,9} = 6.27$, $p < 0.05$) directions (Figure 3.4b). Conversely, Figure 3.5a demonstrates that AMP computed in both medial-lateral and anterior-posterior directions was significantly greater for infants than adults (medial-lateral $F_{1,9} = 15.28$, $p < 0.01$; anterior-posterior $F_{1,9} = 21.67$, $p < 0.01$). Similarly, AMP_{VAR} was significant in both medial-lateral ($F_{1,9} = 19.84$, $p < 0.01$) and anterior-posterior ($F_{1,9} = 24.35$, $p < 0.01$) directions wherein, infants showed higher variability than adults (Figure 3.5b). No effects were observed for Age in either AMP_{TL} or LAG_{TL}.

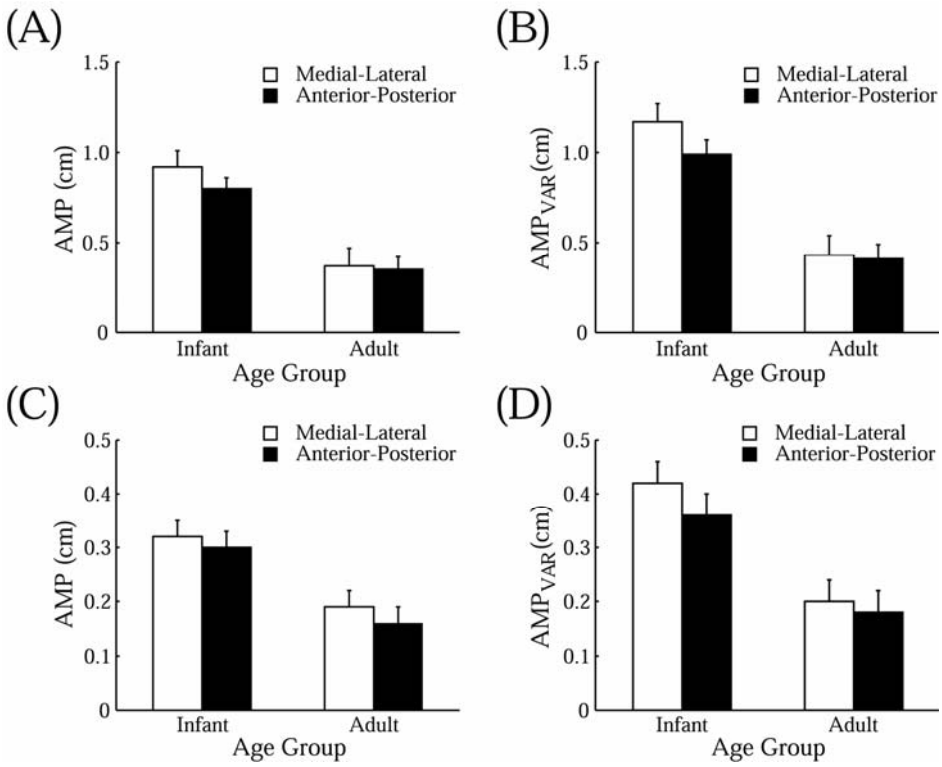


Figure 3.5. Age main effects for (A) total sway AMP, (B) total sway AMP Variability, (C) 0.3 Hz sway AMP and (D) 0.3 Hz sway AMP Variability. In all plots, medial-lateral is plotted with white bars and anterior-posterior with dark bars. Bars represent $M \pm S.E.$

0.3 Hz Sway. The pattern of results in the 0.3 Hz sway was similar to, but had a further interaction than that observed in total sway. For these narrow band-pass filtered data, a significant Age × Condition interaction was revealed for CC_{TL} in the medial-lateral direction ($F_{1,9} = 9.09$, $p < 0.05$). Figure 3.6 illustrates this interaction, wherein adults showed a much larger increase in medial-lateral CC_{TL} from static to dynamic conditions than did the infants.

Follow-up comparisons using Dunn's method performed within Age indicated that while the increase in adults was significant ($t_9 = 5.27$, $p < 0.01$) from static to dynamic conditions, the same was not true for the infants ($t_9 = 1.29$, $p > 0.05$). Because of

the orthogonal nature of this Age x Condition interaction, main effects for medial-lateral CC_{TL}, which were found for both Condition and Age, will not be discussed further.

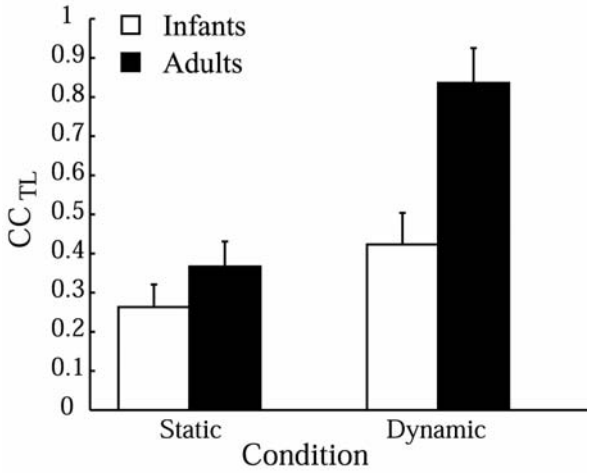


Figure 3.6. Medial-lateral time-locked correlations for infants (white bars) and adults (dark bars) plotted across condition (static, dynamic). Bars represent *M* ± *S.E.*

In the anterior-posterior direction, Condition main effects were observed for the time-locked measures CC_{TL} and AMP_{TL}. A significant Condition effect for CC_{TL}, which reflects phase consistency for 0.3 Hz sway (see Method), was observed in the anterior-posterior direction ($F_{1,9} = 14.07$, $p < 0.01$; dynamic = 0.48 ± 0.05, static = 0.20 ± 0.04). For AMP_{TL}, main effects for Condition were also observed in both the medial-lateral ($F_{1,9} = 8.21$, $p < 0.05$) and anterior-posterior directions ($F_{1,9} = 11.95$, $p < 0.01$). Across age group, AMP_{TL} was greater in the dynamic (medial-lateral = 0.16 ± 0.06 cm; anterior-posterior = 0.12 ± 0.02 cm) than in the static (medial-lateral = 0.07 ± 0.04; anterior-posterior = 0.05 ± 0.01 cm) condition.

Age main effects were again seen within the 0.3 Hz sway for AMP, AMP_{VAR}, and CC_{TL}. Measures of both AMP (Figure 3.5c) and AMP_{VAR} (Figure 3.5d) demonstrated larger values for infants than adults. For 0.3 Hz AMP, infants showed larger sway amplitude than adults (medial-lateral $F_{1,9} = 10.42$, $p < 0.01$; anterior-posterior $F_{1,9} = 9.23$,

$p < 0.05$) with a corresponding increase in AMP_{VAR} (medial-lateral $F_{1,9} = 15.85$, $p < 0.01$; anterior-posterior $F_{1,9} = 9.02$, $p < 0.05$). For CC_{TL}, which showed a significant Age x Condition interaction in the medial-lateral direction, infants had consistently lower values than adults in the anterior-posterior direction ($F_{1,9} = 5.54$, $p < 0.05$, infants = 0.27 ± 0.04 and adults = 0.40 ± 0.04). No Age effects were observed for AMP_{TL} or LAG_{TL}.

Infants Longitudinally

Longitudinal changes in infants' postural responses were assessed using linear mixed-model regression of all dependent measures across Condition and Walk Age. As with the first analysis step, all measures were examined for both total and 0.3 Hz sway.

Touch Forces. As a check for the possibility of the infants changing their reliance upon the contact surface for mechanical support, the absolute level of vertical touch forces (TF_V) were assessed with a linear mixed-model regression that included Walk Age (in days) and Condition as factors. In this analysis, no evidence was found for differential application of touch force in either stimulus condition or across the 10 month duration of this experiment. Irrespective of walk age and condition, these infants applied 3.84 ± 0.53 N of vertical touch force on the contact surface, which is consistent with previous reports at these walk ages (Barela et al., 1999; Metcalfe et al., in press). As no changes were observed in this variable, it is unlikely to have had a strong influence on our pattern of results and thus will not be discussed further.

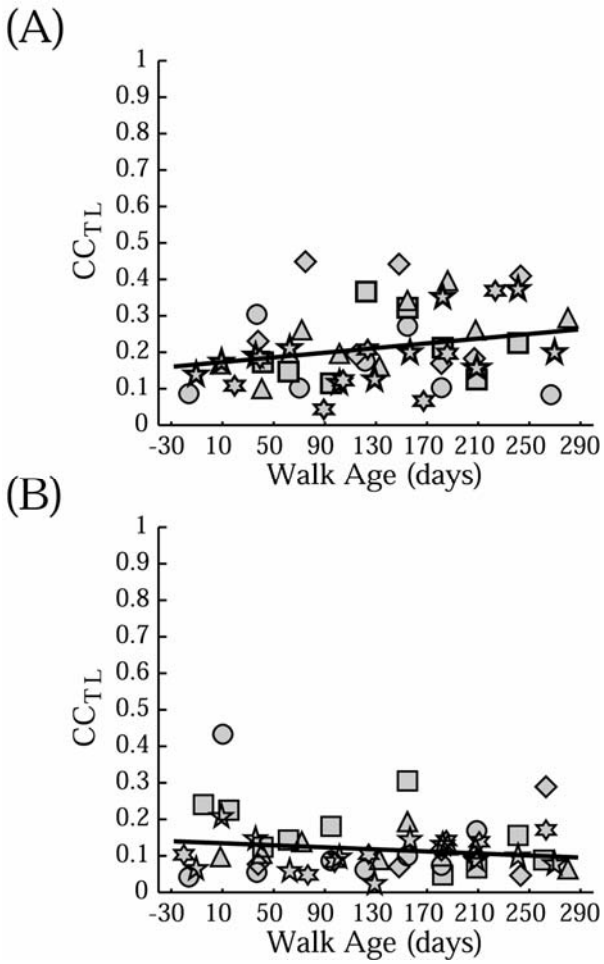


Figure 3.7. Medial-lateral time-locked correlations, CCTL, for all infants in dynamic (A) and static (B) conditions. Separate markers (☆,▽,△,◇,□,○) indicate data corresponding to each individual infant. The solid lines are the mixed-model fits reflecting within- and between-infant sources of variation.

Total Sway. For total sway, significant effects were only observed in the medial-lateral direction. Specifically, Walk Age x Condition interactions were revealed for both CC_{TL} ($F_{1,19.7} = 7.35$, $p < 0.05$) and AMP ($F_{1,19.7} = 4.96$, $p < 0.05$). Figure 3.7a in comparison with Figure 3.7b illustrates that for CC_{TL} this interaction was due to a significant increase across Walk Age in the dynamic stimulus condition (slope = 0.0003 ± 0.0001; $t_{46.8} = 2.28$, $p < 0.05$) that was not observed in the static condition, which had a mean coefficient of 0.12 ± 0.01 across the range of Walk Ages observed. While the Walk Age × Condition interaction was also significant for medial-lateral AMP, neither of the

within-condition slopes alone contributed to this effect. Plotted in Figures 3.8a and 3.8b, the two conditions were differentiated such that, across Walk Age, medial-lateral AMP tended to decrease in the dynamic condition while it increased in the static condition. On a qualitative level, however, this interaction does not appear to have any practical significance.

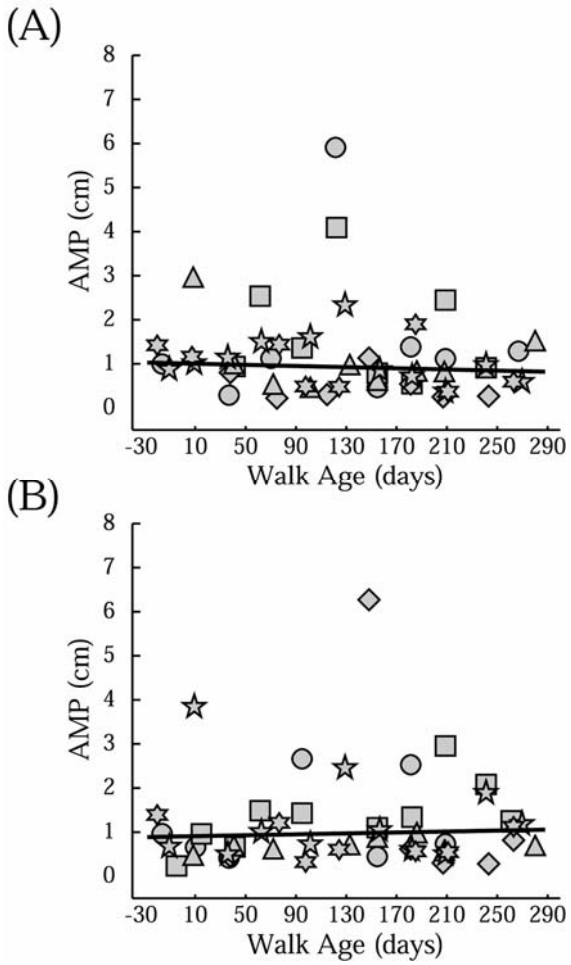


Figure 3.8. Medial-lateral sway amplitude, AMP, for all infants in dynamic (A) and static (B) conditions. Separate markers (☆,▽,△,◇,□,○) indicate data corresponding to each individual infant. The solid lines are the mixed-model fits reflecting within- and between-infant sources of variation.

0.3 Hz Sway. Unlike the findings for total sway, main effects rather than interactions were found for the narrow band-pass filtered 0.3 Hz sway. The only main effect for Walk Age was observed for AMP in the anterior-posterior direction ($F_{1, 56.8}$ =

4.16, $p < 0.05$). Across the 10 months of walking experience, AMP reflected an average increase in anterior-posterior sway of 0.003 ± 0.001 cm/day ($t_{56.8} = 2.04$, $p < 0.05$) for all infants. In the medial-lateral direction, a main effect for Condition was observed for time-locked amplitude ($F_{1, 27.5} = 5.19$, $p < 0.05$) such that AMP_{TL} reflected an increased 0.3 Hz sway in the dynamic (0.15 ± 0.02 cm) as compared with the static condition (0.10 ± 0.01 cm), indicating a consistent within-trial effect of the stimulus on sway amplitude that persisted across all levels of Walk Age.

Discussion

The changing integration of somatosensory information with the postural system was examined in infants as they stood quietly while touching a contact surface that was either stationary or gently oscillating in the medial-lateral direction. The results indicated that infants not only used cues from the contact surface for postural control, but that this integration improved with upright locomotor experience. The comparison of infants with adult controls who performed analogous tasks revealed marked differences between the two groups, as well as evidence for an influence of the dynamic stimulus on the posture of the infants. Most important, these data demonstrated the strongest longitudinal change in the phase consistency, as opposed to the amplitude, of the sway response that was associated with increased walking experience. This supports the general hypothesis that dynamic experience in the upright affords infants opportunities that facilitate the improvement of the ability to estimate body position relative to the environment.

Infants vs. Adult Controls

Comparisons of infants at 6-months of walking age with adult controls demonstrated that infants integrate postural sway with dynamic somatosensory stimuli.

By separately examining within-trial phase and amplitude components of the sway response, evidence indicated that changes in infant sensorimotor integration were primarily due to increasingly consistent phase. These findings were similar to and in the same direction as data from the adult controls that performed an analogous task. Together, the infant and adult data lend credence to the hypotheses that infants integrate dynamic somatosensory stimuli with their sway and that developmental changes are due to increased phase stability by 6 months of walking experience.

Analysis of the sway response in the medial-lateral direction revealed differences between infants and adults in several measures including: AMP, AMP_{VAR}, and CC_{TL}. The finding of increased AMP for both total and 0.3 Hz sway, which are analogous to standard measures of sway amplitude (total sway) and spectral amplitude (0.3 Hz sway), is consistent with previous research with toddlers (2-3 years); that is, infants demonstrated larger sway amplitude than adults (Newell, Slobounov, Slobounova, & Molenaar, 1997; Riach & Hayes, 1987). Also consistent with the results of Riach & Hayes (1987), the AMP_{VAR} results suggest that the infant's large sway amplitude was accompanied by a large within-trial amplitude variance. While AMP and AMP_{VAR} are sensitive only to amount of sway, the time-locked measures offer somewhat different insights. For example, because CC_{TL} is sensitive to within-trial phase stability, it provides a measure of how consistently the individual swayed with the temporal properties of the stimulus. In this experiment, CC_{TL} revealed a Condition effect for total sway indicating that both the infants and adults entrained their medial-lateral postural sway with the stimulus. For the 0.3 Hz sway, however, an Age × Condition interaction revealed that only adults achieved phase consistency in the 0.3 Hz component of medial-lateral sway.

The discrepancy between these two findings suggests that the infant's response to the stimulus was non-linear; that is, the infant's sway response was distributed across the frequency spectrum rather than simply reflecting the 0.3 Hz stimulus in the 0.3 Hz response component. Taken together, the medial-lateral results support sensorimotor integration through consistent phasing of the response to the stimulus rather than stimulus related amplitude increases.

Sensorimotor integration was more clearly observed in infant, as well as adult, anterior-posterior sway. For 0.3 Hz sway both AMP_{TL} and CC_{TL} revealed main effects for Condition, providing evidence for infant and adult sensorimotor integration. For total sway, a CC_{TL} main effect for Condition also supports consistent phasing between anterior-posterior sway and the stimulus. Further, the Age effects observed for amplitude measures were similar, but in general smaller, than the same effects in the medial-lateral direction. The finding of Condition effects in the anterior-posterior direction across the age groups is consistent with previous data for this type of postural task. A medial-lateral stimulus is typically associated with a postural response in the same direction. However, we have observed that this effect is dependent in part on the position of the touch apparatus relative to the individual's base of support. That is, in cases where the stimulus presented to the hand has required an arm position forward and to the side of an individual standing in parallel stance, effects could be observed in anterior-posterior sway (Jeka, Ribeiro, Oie, & Lackner, 1998). As such, we intentionally placed the touch apparatus for adults in a location that was analogous to the infants and found anterior-posterior effects in both age groups. Additionally, the use of parallel stance may have led to decreased anterior-posterior stability. The finding of similar statistical effects but

decreases in overall amplitude and phase stability of the anterior-posterior rather than medial-lateral sway suggests that the anterior-posterior direction was a smaller and less stable component of the overall sway. Thus, the effects of the stimulus appeared stronger in the anterior-posterior direction due to this lower baseline stability. Taking all of these factors into account, the clear effects in the anterior-posterior sway for both adults and infants further validate the conclusion that the infants demonstrated an ability to integrate the somatosensory stimulus with their postural control system.

Previous research on visual manipulations of the environment suggest that prior to walking onset, infants responses to dynamic visual stimuli while in a seated posture are characterized by an inconsistent within-trial phase relationship (Barela et al., 2000). We observed that both the adults and 6 month walkers demonstrated consistencies in the phase relationship with the stimulus. These data point to clear signatures of integration between the sensory cue and the postural control system. While the current data alone cannot address whether amplitude and phase relationships develop differentially, taken in the context of the previous research (Barela et al., 2000; Clark et al., 1988; Konczak et al., 1995; Sokol et al., 1992; Wiener-Vacher et al., 1996), these data contribute to understanding sensorimotor integration by showing improved phase, as opposed to amplitude, consistency in infants by 6 months of walking experience.

Infants Longitudinally

The comparison with adults performing an analogous postural task established that by 6 months of walking experience these infants were capable of adopting a temporally consistent relationship with the somatosensory stimulus, particularly in the anterior-posterior direction. In the second step of this analysis, the goal was to probe

developmental changes in this sensorimotor integration as a function of upright postural experience from the onset of independent walking. Thus, all infants were assessed using the same event-related measures in both the static and dynamic conditions from 1 month prior to walk onset until 9 months of walking experience.

The longitudinal analysis revealed the infants' postural responses showed increasingly stable phase in the medial-lateral direction with walking experience. Specifically, because time-locked correlations (CC_{TL}) are influenced by phase consistency and because this measure was sensitive to longitudinal change, it was concluded that changes in this sensorimotor integration are due to increasingly stable phase responses to the dynamic stimulus. While, for medial-lateral AMP a Walk Age × Condition interaction between reached statistical significance, qualitative assessment suggested that this effect may not have any practical significance (Figure 3.8). By contrast, Figure 3.7 displays an obvious effect such that prior to walk onset the estimated regressions did not differ across condition (compare CC_{TL} at Walk Age = -30 in Figures 3.7a & 3.7b), indicating a lack of phase consistency that improved with increased walking experience.

This constellation of observations taken in combination with the information, albeit sparse, hinting that the temporal aspects of stimulus-induced postural responses is highly variable prior to walk onset at both the level of behavior (Barela et al., 2000) and muscular activation (Sveistrup et al., 1996), suggests that the phase stability may develop concurrent with walking experience. What underlies the relationship between locomotor experience and this changing phase consistency, however, remains to be fully understood. One suggestion may be derived from the fact that, similar to the medial-lateral results

from the adult versus infant comparison, the longitudinal data indicated nonlinearities in the development of sensorimotor integration. That is, effects associated with walking experience were found in total rather than 0.3 Hz sway. What this indicates is a lack of precision in adopting the appropriate temporal coordination between postural sway and the information specified by the stimulus.

A precisely defined temporal relationship between body sway and sensory stimuli is necessary for veridical estimation of body position relative to the environment. While this estimation of postural state is considered integral in control-theory based models of posture for adults (Kiemel, Oie, & Jeka, 2002; Kuo, 1995; Lestienne & Gurfinkel, 1988; van der Kooij, Jacobs, Koopman, & van der Helm, 2001), its role has, until recently, had minimal influence on explanations of postural development. In part, this is due to a lack of investigations identifying how the specific properties of the stimulus may interact with different sensory modalities to influence the nature of infant's postural responses. For example, prior assessments of the frequency response characteristics of adult posture have led to the suggestion of modality-specific use of position versus velocity cues in the sensorimotor control of posture (c.f. Dijkstra, 2000). Recent theoretic modeling (Kiemel et al., 2002) has further indicated the importance of velocity information for the formation of stable estimates of postural state. The finding of improvements in phase consistency in the current study indicates a changing ability to stabilize the temporal aspects of postural coordination with external environmental information (see also Metcalfe et al., in press) and thus, is consistent with conclusions regarding the interaction between upright walking experience and the ability to utilize somatosensory cues for prospective estimation of body position relative to the environment (Barela et al., 1999).

These arguments further reinforce the conclusion that infants in this period of ontogeny exploit the opportunities provided by upright walking experience to actively tune their sensorimotor relations for adaptive stance control (Metcalfe & Clark, 2000). Future investigations, however, will aim to more thoroughly characterize the nature (e.g. frequency response) of this type of sensorimotor integration across development as well as how the role of state estimation changes in concert with other aspects of stance control.

Event-Related Time-Frequency Analysis

The method used in the present study was adapted from event-related and time-frequency analyses used in the EEG literature. These types of analyses have proven useful to uncover cortical signatures of a variety of motor and cognitive-motor tasks including simple finger and toe movements (Pfurtscheller, Neuper, Andrew, & Edlinger, 1997), choice reaction time tasks (McDowell, Jeka, Schöner, & Hatfield, 2002), and elite marksmanship (Kerick et al., 2001). The strength of these techniques is that they discriminate specific components of a signal embedded within noisy data. While this has not been a major problem for postural research with adults, due to relatively high-gain sway responses to dynamic stimuli, this is a more relevant issue when attempting to understand the infant's dramatically more variable postural sway. In the present study, the number and the consistency of the effects suggest that event-related time-frequency analysis was a powerful tool for examining dynamic aspects of infant posture across development. The method was further validated by the fact that the same general pattern of results was observed in the measures based on total sway and 0.3 Hz sway, providing a strong indication that the observed sensorimotor relationship was not merely an artifact of the narrow band-pass filter at the stimulus frequency.

As this study was an initial foray into applying such techniques to the problem of infant posture, future research may be guided by the results of this exploratory effort. For example, in the present study, time-locked correlation appeared to be the measure that was most sensitive to age and condition effects on sensorimotor integration. In part, the correlations were advantageous because they were computed on approximately double the number of cycles as the time-locked measures of amplitude. In studies such as this, where participants entrain to periodic stimulus with a specific frequency, this is a relatively powerful measure and thus will be useful in future characterizations of infant posture across a range of stimulus properities.

Conclusions

In this study, we observed convincing evidence that infants adopted a consistent relationship between their postural sway and a somatosensory stimulus following onset of independent walking. Further, the temporal stability of this relationship increased concurrently with increasing walking experience. This observation is consistent with the hypothesis that the ability to integrate a sensory cue into the postural response and the ability to estimate relative body position develop differentially in time. Marked differences between the postural responses of adults and infants with 6 months of walking experience were also observed. In particular, changes in overall postural stability, as well as task and stance-specific stability, influenced the manner in which infants used the stimulus to control upright standing and stabilize phase relations. Future investigations of this developing sensorimotor relationship, across the lifespan as well as at multiple levels of analysis, would benefit from further assessment of the differential development of amplitude and timing components of postural sway across a range of

dynamic sensory environments. Insights from such investigations will provide the information necessary to understand how infants tune their sensorimotor relations for the development of stable estimates of body position in space, thus leading to increased capacity for adaptive stance control.

Chapter 4

Computational Representations of Posture and its Development

In this chapter, the constraints on independent, upright stance are discussed through the example of the inverted pendulum. We begin by describing the inverted pendulum without stabilizing influences and then systematically build towards an actively-controlled system. To facilitate this discussion, we review some of the models that have appeared in literature on postural control in the human adult with a focus on how we can develop predictions and explanations regarding human postural development. Following this review, we examine the performance of a computational model of learning to remain upright under a variety of changing constraints that are representative of those faced by the human learning to stand for the first time. In particular, in Chapter 5 we present a study regarding the manner in which the infant (or the infants' sensorimotor system) decides or learns how to set physiological parameters through the guidance of exploratory action. Accordingly, the primary goal of the current chapter is to provide a backdrop for this study through analysis of model-based expressions of postural control and its development as well as their connection with (and ability to formally examine) known biological changes that occur with learning and physical maturity.

Herein we will examine the aspects of postural development that result in stabilization of overt postural sway through the period where the infant 'solves' the problem of remaining upright. Albeit a rather coarse level of control, by approximately 9 – 10 months, the human infant manages to remain standing for relatively short epochs of time. As presented in chapter 2, as well as in other works from our research group (Chen

et al., 2007a; Metcalfe & Clark, 2000), we have observed that newly walking infants are capable of independent (i.e. unassisted) upright posture in epochs of at least 10 seconds. So, of course, the question that we ask is: 'What is it that changes throughout and following the transition to independent stance and locomotion?' Or, more to the point, 'How do the various constraints interact to produce increased stability in postural control with the accumulation of experience in the upright?' In order to answer this question, we begin by delineating definitions of the task and provide a formal expression of what it means to stabilize posture.

A model of what? A description of "the problem of posture"

Stability is defined based on two criteria: pattern consistency, marked by low variability, and pattern robustness, marked by resistance to perturbation. By these criteria, the newly standing infant may have achieved the basic capacity to maintain an upright position, however extant data suggest that their overall posture remains largely unstable. That is, the newly standing and walking infant demonstrates marked levels of variability in their sway that is characterized by control that lacks robustness in the face of either sensory or mechanical perturbation. Further, while our data have revealed that the magnitude of variability remains consistent across the first year of walking experience, at least at the level of the center of pressure and center of mass (Chen et al., 2007a; Metcalfe et al., 2005a; Metcalfe & Clark, 2000), others have shown an increasing capacity to respond to sensory and mechanical perturbations with increased experience in the upright posture (Forssberg & Nashner, 1982; Foster et al., 1996; Hadders-Algra et al., 1996; Hadders-Algra et al., 1998; Sveistrup & Woollacott, 1996). Therefore, we may surmise that after the infant has achieved a basic level of independent stance control, she

or he will go about stabilizing their sway by first enhancing the 'robustness' and later, during toddlerhood and beyond, will reduce the magnitude of variability (Newell et al., 1997; Newell, 1998). Indeed, this seems an intuitive 'strategy' to most efficiently solve the problem of learning to avoid falling over. That is, as a first approximation to a solution, we may enhance our general ability to remain within the region where we will not fall, meaning we learn the edges of the behavioral state space first, and then, once the goal of maintaining an upright posture is met, the toddler will proceed to improve and refine that behavior towards achievement of a different goal. For example, perhaps in the long run a better solution is to maintain stance in a manner that minimizes energy expenditure; thus requiring learning to control sway with a different spatial referent (e.g. consistently staying closer to vertical and swaying less in order to minimize the torque due to gravity acting to pull the infant to the ground).

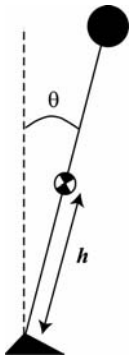


Figure 4.1. A basic representation of human stance as a single segment inverted pendulum. The vertical dashed line represents the desired state with respect to gravity ($\theta = 0$), the ☢ represents the location of the total body center of mass, the force of gravity acting at the center of mass (e.g. weight) is equal to mg (m = mass of the body, g = acceleration due to gravity) and height above the ankle is equal to h.

Since this dissertation aims to understand the stabilization of infant sway behavior, it is useful to assess an already well-known system that is mechanically analogous to the upright standing human. Because we seek to examine a mechanical

system that is intrinsically unstable – as is the upright human – we accept the commonly used inverted pendulum model (Figure 4.1). Equation 4.1 describes the inverted pendulum as a system that experiences a destabilizing torque about the ankle that is proportional to the torque due to gravity acting on the pendulum. The gravitational torque (aka. the disturbance torque) is caused by the vertical force of the body weight (mg; m = body mass, g = gravitational acceleration) acting at the center of mass (CM) of the body located at height, h above the ankles and with the horizontal moment arm that is proportional to the angular displacement from vertical (θ).

$$I_b\ddot{\theta} = mgh\sin\theta \qquad (4.1)$$

The left hand side of equation 4.1 shows that this disturbance torque about the ankle can also be characterized through an angular adaptation of Newton's law of acceleration ($F = ma$) by the moment of inertia of the body (I_b) multiplied by the rotary acceleration experienced by the pendulum ($\ddot{\theta}$). A moment of inertia for a mass rotating about an axis is defined as the cumulative sum of the mass in the body as a function of its spatial distribution with respect to the axis of rotation and this value quantifies the magnitude of the bodies resistance to angular acceleration. A simplified representation for the moment of inertia is

$$I_b = mh^2 \qquad (4.2),$$

The term mh^2 derives from the parallel-axis theorem (Enoka, 2002) and indicates the influence of force applied at the center of mass as it affects a torque about the axis of rotation, in this case, the ankle. Given Equation 4.2, we can re-organize Equation 4.1 as follows:

$$\ddot{\theta} = \frac{mgh\sin\theta}{mh^2} \qquad (4.3)$$

Equation 4.3 now demonstrates that the actual motion of the inverted pendulum (its acceleration), without any other mechanical elements to provide stabilizing forces/torques, is directly proportional to the displacement from vertical. As the rotary displacement of the body increases with respect to vertical, so will the angular acceleration; a phenomenon directly related to an increase in the length of the horizontal moment arm of the disturbance torque as deviation from vertical increases. More important to this dissertation, the acceleration is *inversely* proportional to the relative height of the whole body center of mass above the ankle (*h*). This inverse relationship states that a taller pendulum will fall through its angular range more slowly than will a shorter pendulum.

As should be clear, the inverted pendulum is a simple, yet compelling model for describing the problems associated with postural sway because of its intuitive connection with the challenges of upright stance. Both the inverted pendulum and the upright human are intrinsically unstable due to balancing a top-loaded mass over a small support base. Further, the mathematical relations above provide a backdrop for identifying an important task constraint - learning to remain close to vertical to keep the influence of gravitational force to a minimum. This model additionally leads to a simple explanation of the 'slowing down' effect that has been observed across increasing walking age (Chen et al., 2007a; Metcalfe et al., 2005a). That is, because the child is in a period of physical growth, one would predict that the body naturally reduces the speed of its postural sway (McCollum & Leen, 1989).

Stabilizing influences

Passive versus active stabilization. In order to remain upright, the inverted pendulum requires additional help to counteract gravitational (and other) forces leading to an overall disturbance torque around the ankles. One such stabilizing influence is that humans have feet. In particular, the feet change the dynamics of the system because they allow the individual to utilize ground reaction forces to corral the body within certain stability limits. The limits, of course, are constrained by the length of the feet and further, foot size interacts with pendulum height such that as a person gets taller while foot size remains the same, she or he will have a smaller permissible range of sway. If foot length remained constant while growth in height ensued, then the permissible range of sway would reduce by an amount predicted by changes in height alone. Conversely, if the foot length increased in direct proportion to growth in height, the range of sway that is structurally permitted would remain constant across development. Available data (and common sense) suggest that neither of these scenarios are consistent with reality; that is, the increase in height of the center of mass outpaces changes in foot length during the first two years of life[8]. Owing to this structural constraint (the length of the foot relative to center of mass height), one would predict that sway range would decrease with growth.

A second source of mechanical stabilization involves the viscoelastic nature of the muscles and tendons crossing each joint. If these tissues are stiff enough, the restoring forces generated by their stretch will lead to a stabilizing torque of large enough magnitude to counteract the overall disturbance torque and passively balance the system.

[8] Specifically, linearly regressing center of mass height on foot length reveals a slope of 3.4. Data for this regression were estimated from the following sources of anthropometric data: for foot length changes, data were obtained from the Anthrokids project (Ressler, 1977) and specifically, the data file located at http://www.itl.nist.gov/iaui/ovrt/projects/anthrokids/data1977/586.xls; center of mass data were obtained from (Palmer, 1944 tables 9 and 10).

Taken a step further and assuming CNS regulation of muscle stiffness, this becomes the 'stiffness control hypothesis' that was initially articulated by Winter and colleagues (Winter et al., 1998) who later attempted to validate their hypothesis with empirical measurement of ankle muscle stiffness (Winter et al., 2001). Including the restoring force due to ankle stiffness (- $K\theta$) in the model for the single segment inverted pendulum yields:

$$I_b\ddot{\theta} = -K\theta + mgh\sin\theta \qquad (4.4)$$

Similar to how gravitational force induces the disturbance torque, the restoring force about the ankle joint due to musculotendious stiffness will increase as a function of displacement from equilibrium. As Winter (1998) argues, so long as the value of stiffness is large enough (K must exceed mg) the system will oscillate with an undamped natural frequency (ω_n) equal to:

$$\omega_n = \sqrt{\frac{K - mgh}{I_b}} \qquad (4.5)$$

Here we make two further observations that provide clues about mechanisms for postural development. First, a decrease in stiffness would directly result in a decrease in the natural sway frequency; an effect consistent with that predicted by increasing height. Second, we note that the moment of inertia in the denominator is also consistent with our prior observation of an inverse relationship between center of mass height (recall, $I_b = mh^2$) and angular acceleration. However, as depicted in Equation 4.5 frequency decreases as a function of the square root of $\frac{1}{h^2}$ (assuming all other terms are held constant) which means that the reduction in frequency with increasing height occurs at a slower rate than the reduction in acceleration with increasing height. More important, this discussion

serves to show how the same type of change, slowing down of postural sway, can be due to several changes in the passive mechanics of the body alone (increased height, decreased stiffness, or increased height combined with decreased stiffness). Therefore, this is a clear example of how empirical observation of the resultant behavior, on its own, is insufficient to allow inference of sources of change with development.

Although our explanation to this point has provided some detailed insights into the mechanical nature of postural development, it remains a bit oversimplified and neglects the known role of sensory information on the maintenance of upright stance. Visual, vestibular and somatosensory modalities each provide information that is partially unique from and partially redundant with information provided by the other modalities. Ideally, all three sensory modalities present the CNS with veridical information regarding the current state of bodily motion relative to the environmental motion. Indeed, it has been well documented that postural stability is significantly compromised when the information provided by one or more senses is degraded or otherwise rendered unreliable (Horak et al., 1990; Nashner, 1976; Nashner & Peters, 1990; Woollacott et al., 1986). Currrently, it is understood that fusion of information coded by each modality is critical for resolving perceptual ambiguities in estimating self- versus environmental motion and thus, is also critical for the *adaptive* control of stance across a wide variety of task and environmental circumstances (Berthoz & Viaud-Delmon, 1999; Buchanan & Horak, 1999; Horak & MacPhearson, 1996; Jeka et al., 2000; Kiemel et al., 2002; Oie et al., 2002).

The modern understanding of upright stance control is that sensory information is not only critical for organizing *responses to external disturbances*, but is integral for the

online, continuous stabilization of unperturbed stance. Postural behavior reflects the functioning of an integrated sensorimotor control system and should be studied as such. This type of thinking is part of the basis on which the 'stiffness control hypothesis' has been challenged. Operating from a perspective that considers sensory information integral to the stabilization of posture, Morasso and colleagues used a model-based analysis to demonstrate that although passive ankle stiffness provides a significant stabilizing influence, it alone is inufficient to stabilize human upright stance (Morasso et al., 1999; Morasso & Sanguineti, 2002; Morasso & Schieppati, 1999). Such theoretic claims have been recently supported by direct, microscopic-level observations of muscular length changes during postural sway that indicated 'paradoxical' length changes inconsistent with spring-like contributions to stance corrections (Loram et al., 2005). These types of developments in the understanding of human postural control are making a strong case that passive mechanics alone are unable to explain postural control completely. Active mechanisms are required for regulating online stance corrections within a dynamic environment as well as accounting for known transmission delays in the sensory feedback loops of the nervous system. By specifying appropriate motor commands to the right muscle groups at the right time, the human is capable of actively responding to perturbations as well as making adaptive online control decisions.

Models of active mechanisms for postural stabilization. While a thorough review of the literature involving the modeling of the human postural control system is beyond the scope of this dissertation, it is important that we discuss at least two general types of mechanistic models that have inspired significant insights into the nature of sensorimotor integration embodied in upright stance control. The interested reader, however, is referred

to (Kiemel et al., 2002) for a detailed mathematical analysis of several control theory based models as well as (Dijkstra, 2000) for a review of models that characterize sensorimotor coupling without the mechanical constraints associated with the physical structure of the body. For the purposes of this dissertation, however, we restrict our attention to those models that *include* mechanical constraints in order to account for physical influences, such as growth, on postural stabilization during early development.

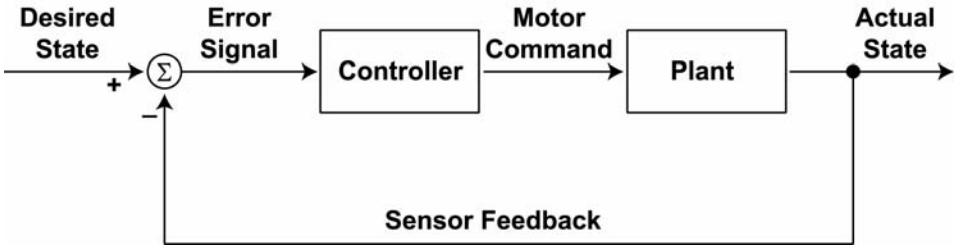


Figure 4.2. A schematic representation of a general closed-loop control system.

What the two types of models that we review have in common, in a very general sense, is that they distinguish various system sub-components and attempt to characterize how each influences the overt behavior of the system. Figure 4.2 shows a block diagram characterizing the basic elements of a closed-loop control system. Such a system typically includes (a) the mechanical system ('plant'; body dynamics), (b) sensor feedback of the actual, as opposed to commanded, state of the plant, (c) a comparator that generates an error signal based on the difference between the current state and an internally-represented desired state and finally, (d) the controller that generates the next commands to be issued based on the error signal. While models vary in the specifics of how these elements are instantiated, these 'blocks' allow investigators to make precise mathematical statements about the different influences on the behavior of the system as well as relations between them (see Jordan, 1996 for review).

Servo-control mechanisms are commonly classified based on the type of feedback used to generate motor commands. Specifically, models of this type utilize some combination of proportional (P), derivative (D) and/or integral (I) feedback error in order to issue appropriate corrective motor commands. This means that motor commands are specified either as a proportion of the overall magnitude of error (e.g. absolute position error), the derivative, or rate (e.g. velocity) at which position error changes or, finally, the time integral of constant error (e.g. cumulative error) signaling the existence of a steady-state bias. The influence of proportional feedback typically is rapid movement of the system from its current position to its desired position, whereas derivative feedback acts to damp the system and prevents overshoot of and/or oscillations around the target position. Because of the inertial properties of the human body, PD feedback is minimally necessary if the system is to be stabilized (Morasso et al., 1999). There is some question whether the integral term, which functions on a longer time-scale than either proportional or derivative feedback, is necessary for the adaptive control over posture. Those who choose to include it do so on the basis of observations of long time-scale dynamics that can not be captured in the simpler PD model (c.f. Johansson et al., 1988).

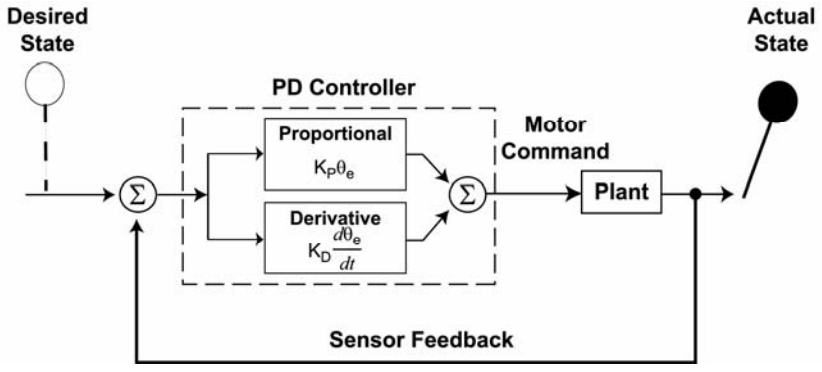


Figure 4.3. A schematic representation of a servo-control system that utilizes PD feedback regarding the error (θ_e) between desired and actual state. The terms K_P and K_D represent the gains (weightings) on proportional (position) and derivative (velocity) feedback, respectively.

Figure 4.3 provides a simplified representation of a control system that utilizes proportional and derivative feedback. Here we see 'inside' the controller, wherein the two types of feedback are differentially weighted in their contribution to the motor command. These weightings, or gains, determine both the magnitude of corrections and the time-scale over which the corrections are made. For example, if a given system is inappropriately biased towards high position feedback by having a large proportional gain coupled with a low derivative gain then it would likely have a rapid response that overshoots target position and further, takes a long time to settle at an equilibrium point (i.e. similar to what happens when a newly-standing infant experiences an unexpected perturbation). Conversely, if the derivative gain is set too large relative to the proportional gain, the system would be 'overdamped' and it would become nearly impossible to actually reach the desired equilibrium position. Thus, refined control in a servo-control system involves, in part, correct specification of the feedback gains.

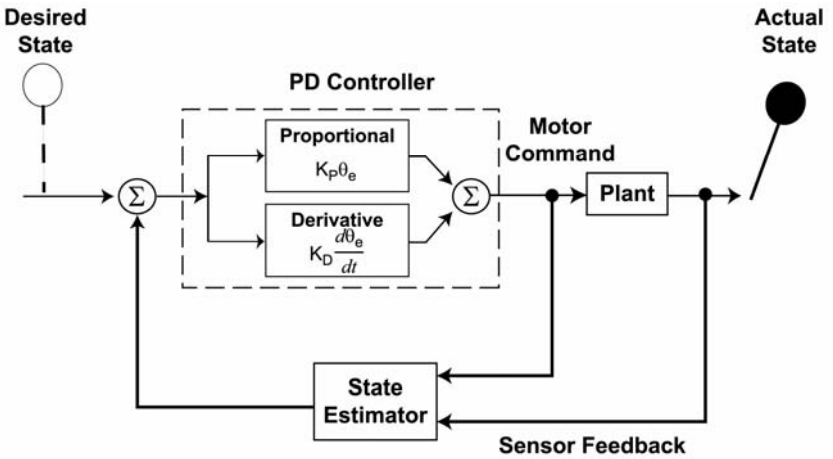


Figure 4.4. A schematic representation of an optimal-control based system that uses a state estimator to help generate the error signal that is fed into a PD controller. Depicted here, the state estimator utilizes information from the sensor measurements as well as the motor command that was issued to generate an estimate of current state that is output to the comparator that then determines the error signal for the controller. .

There is one critical assumption associated with servo-systems of the type described above that may or may not be tenable in the biological control system for human stance. In particular, it is assumed that the sensor feedback is 'error-free' and correctly specifies current system state. Models rooted in optimal control theory, on the other hand, do not necessarily take this assumption for granted (Kiemel et al., 2002; Kiemel et al., 2006; Kuo, 1995; Kuo, 2002). Of particular concern to those who utilize such models is the process by which current state is estimated, rather than directly sensed, through partially veridical sensory information. In other words, when implementing models involving state estimation, it is acknowledged that there is some random variation, or noise, associated with neural transmission of sensory information in addition to the noise associated with neural computations and motor commands. Typically, the problem of state-estimation is realized in optimal control models through use of a Kalman filter that is capable of taking a history of noisy-sensory estimates along with the control signal and outputting an optimal estimate of current system state. Figure 4.4 provides an exemplar block diagram of a feedback control system that includes a state estimator.

Developmental questions

All theorizing considered, but temporarily set aside, our understanding of human development must ultimately answer to, or be constrained by, empirical observations of actual human behavior. As such, it is worthwhile to summarize the major behavioral and structural changes that should factor into a model that captures 'postural development'. Thus far, we have established the challenges that the task of maintaining upright stance presents the human. An analogy has been drawn between the human body and an

inherently unstable inverted pendulum. Likewise, quiet stance behavior has been likened to a system that establishes an 'unstable equilibrium' through a mixture of passive mechanical factors and active feedback-control mechanisms. With this backdrop, we ask where in these models is room to hypothesize things that precipitate change with development.

The first and most obvious source of change is that with increasing age, infants grow, gain weight and redistribute body proportions. Further, the multi-articulated human frame has muscles crossing each joint that, even in the absence of neural activation, act to damp the system as well as develop restoring forces via spring-like load-deformation properties. Therefore, the physical structure of the body is one primary contributor to human postural behavior and further, as it changes with growth and development it is likely that the observable movements of the body would also take on new or modified characteristics.

A second possible source of developmental change is that muscles change as a function of physical maturation as well as habitual use (Sale, 1987). With respect to physical maturation during infancy, muscles get bigger and the distribution of fiber types composing muscles shifts towards an increased density of 'slow-twitch' or 'slow oxidative' fibers (Malina et al., 2004). In general, across the first two years, such changes are manifest in a tendency of muscles to take on increasing slow-twitch characteristics such as increases in tension rise time (time to peak tension) as well as increased relaxation time (time for muscle activity to settle to a stable, commanded activation state state). Thus, it seems that the body not only mechanically slows as a passive result of growth, but it also reduces the rate of tension production by the musculature in favor of

fiber types (and properties) that tap more energy-efficient oxidative, as opposed to glycolytic, mechanisms.

As we begin to consider known chronic adaptations due to habitual muscle use, the issue becomes increasingly complex (c.f. Enoka, 2002; Sale, 1987). Consider for a moment the observation that when a novel action is performed, human infants tend to be 'too stiff' due to high levels of muscular co-contraction (in fact, most adults react in a similar manner during the very first trials of a novel action). With increased experience in a task, gains occur both in strength and efficiency in how and when the infant recruits muscles to make stance corrections (Sveistrup & Woollacott, 1997). As such, it is possible that the development of muscle control over a given action has a pattern of reducing the average amount of muscle activity with increased task experience in lieu of more appropriately timed activation patterns (i.e. synergies) that are scaled to the size of the destabilizing influences to be compensated. Consistent with previous observations (Chen et al., 2007a; Metcalfe et al., 2005a) as well as predictions based on increased height (McCollum & Leen, 1989), lower stiffness[9] leads to a slower frequency during quiet stance and likely contributes to slowed responses to external perturbations.

Certainly it is not very far fetched to say the body is only one of several sources of constraint on observable sway behavior. Our previously-discussed depictions of active feedback control open the discussion regarding additional sources of influence over adaptive postural adjustments. For example, we could choose to temporarily entertain the concept that a servo-controller algorithm (e.g. PD/PID feedback) is used to control posture and then ask questions regarding the establishment of appropriate gains

[9] We recognize that joint and/or muscular stiffness and magnitude of muscle activity are not synonymous and do not wish to imply that this is the case. However, with high degrees of co-contraction, it is reasonable to expect that the system responds with a greater amount of apparent or effective stiffness.

weighting the different types of feedback error or, rather, we could follow suit from the adult literature and attempt to assess which types of feedback are necessary[10]. Is it possible that PD control sufficiently explains infant posture whereas it has been shown to only partially describe the posture of adults? If so, then we would predict that the acquisition or emergence of a integral-type feedback control, akin to the PID models examined in the adult literature (Johansson et al., 1988; Kiemel et al., 2002), embodies developmental changes in the use of sensory feedback.

Such a proposition is not entirely implausible and, in fact, may provide a reasonable explanation of the empirical results that were discussed in chapter 2. Specifically, it was argued that the slowing-down effect that we observed could be an indication of stance control based upon longer time-scale use of sensory information. Given that the integral term has come to be considered one of several possible explanations for the long time-scale or 'slow drift' component of adult postural control, such an assertion may be worth consideration. However the results presented in Chapter 3 were interpreted as due to a part of the feedback loop other than the controller algorithm. In conceiving that study, extant results in the literature led us to suggest that early postural responses characterized by large amplitude but poor timing were indicative of extraction of relevant cues from the environment but reflected a poor capability to utilize those cues to regulate sway in an adaptive manner. In part, this lack of temporal stability was proposed to be a signature of poor estimation (Figure 4.4) of self motion. Under that assumption, we predicted that if increased experience in the upright 'tutors' our ability to estimate our own self motion, then we would see enhancements specifically in temporal

[10] Of course, the amount and quality of data typically required for modeling of this type (c.f. Kiemel et al., 2002; Kiemel et al., 2006) poses a significant challenge in the empirical study of human infants that would be required to support such endeavors.

stability with increases in walking experience; a prediction that was borne out in the results of that analysis. Temporal stability of infant responses was indeed improved and subsequently we concluded that this finding was consistent with improvements in estimation. As with the ambiguity regarding passive mechanical influences on observed behavioral changes that was mentioned earlier in this chapter, we again see an opening for model-based analyses to help resolve open questions regarding observations that do not lend themselves to unique interpretations.

Summarily, we have outlined, in somewhat broad strokes, the major constraints that have the potential to explain stabilization of stance with development. Although the body proportions have begun to stabilize by the time of walking onset, changing physical and functional morphology likely continues to facilitate improvements in postural stabilization in the second year of life by increasing inertial properties of the body. While greater inertia means that it is harder to bring about active stance corrections, it is also adaptive in the sense makes the body more resistant to external disturbances. Enhancements in slow-twitch muscle fiber characteristics allow for increased duration of standing before muscles begin to fatigue and give way to gravity, not to mention that such changes slow the development of tension leading to corrective torques. Evidence further suggests that increased experience in the upright is associated with changes in behavior that are consistent with both tuning of feedback gains and/or facilitation of the process(es) associated with state estimation. In reality, postural development likely represents a dynamic mixture of all of these changes, each with its own ontogenetic time-course (Thelen, 1986; Thelen & Smith, 1994). Therefore, the challenge becomes one of finding the appropriate methodology and framework to allow formalized examination of

this dynamic mixture of changes. In the next chapter, a final study is presented that characterizes such an effort; the simulation and modeling of postural development, inclusive of changes in the physical morphology and system parameters.

Chapter 5

The Development of Upright Posture as Characterized by a Continuous-Time, Continuous-Space Reinforcement Learning Model

Introduction

Developmental science has undergone dramatic advances during the last 30 years (Hammock & Levitt, 2006; Thelen, 2000b). Of particular impact has been the increased multidisciplinarity evident in emerging and established collaborations between psychologists, neuroscientists and computational scientists (for examples, see Berthier et al., 2005; Metta et al., 1999; Newell & Molenaar, 1998; Thelen et al., 2005) and the concomitant re-emergence of a process-oriented focus on lifespan change (Clark & Whitall, 1989; Nesselroade & Schmidt McCollam, 2000; Thelen, 2000b). Indeed, as the sheer number of empirical observations regarding human development expands, the need for formal frameworks capable of linking them with theoretical constructs becomes increasingly apparent. This is especially true for fundamental motor behaviors, such as posture and locomotion, that have been studied to an extent that formalized modeling aimed at understanding specific sources of developmental change is becoming increasingly possible. Accordingly, the study described in this chapter examines upright standing using an established computational framework, reinforcement learning (Sutton & Barto, 1998), to initiate the formalized explanation of how changing constraints due to maturation and learning influence postural behavior during its acquisition and subsequent refinement.

The ability to account, in a mechanistic sense, for developmental change in behavior is reliant upon the amount and quality of information in the collective empirical

database. This is especially true when the goal is to articulate formal, model-based statements regarding how a behavior is acquired and refined during development. It has become widely recognized that monolithic explanations of human development have given way to those that consider behavior as emergent from a system of complex, interacting constraints, each of which follow their own ontogenetic progression (c.f. Cairns, 1998; Lerner, 1998; Overton, 1998; Thelen, 1986; Thelen & Smith, 1994; Thelen & Smith, 1998; Valsiner, 1998 for discussion of the evolution of theoretical concepts of development). As a consequence of this shift in understanding, models depicting developmental change necessarily have become either (a) more focused on very specific, proximal constraints underlying a specific behaviors (e.g. Berthier, 1996; Mareschal et al., 1999; Morton & Munakata, 2005) or (b) more complex and reliant upon detailed information about both distal (global) and proximal sources of constraint on the overall behavior (e.g. Kuniyoshi & Sangawa, 2006; Parisi & Schlesinger, 2002). Of course, both types of models are needed and both have (or should have) empirical observations as their foundation.

The acquisition of independent standing has been 'on the charts' of human development for most of the last century (Bayley, 1993; McGraw, 1932; Shirley, 1931). Yet, aside from documenting the relative timing of its acquisition, process-oriented efforts aimed at understanding the *detailed* aspects of human postural behavior did not begin to appear frequently in the developmental literature until the mid-1980s (Reed, 1989). As a result, data regarding specific changes during postural development remain relatively sparse. This knowledge gap is particularly glaring when compared with the

extent (e.g. Horka & MacPhearson, 1996) and level (e.g. Loram et al., 2005) of details that have been recorded about postural behavior in mature adults.

What *has* been shown about infant postural development can be summarized as follows: in general, balance control immediately after the onset of independent standing is rather precarious, so much so that even non-mechanical perturbations have been shown to induce a fall (c.f. Lee & Aronson, 1974). While able to remain upright for brief epochs, infants are highly unstable in their posture through the first 4-6 months of independent standing and progressively become stabilized throughout the first few years of walking experience (c.f. Bertenthal & Clifton, 1998). This persistent postural instability, as well as its subsequent diminution, has been repeatedly demonstrated across a variety of tasks, including unperturbed standing (Chen et al., 2007a; Metcalfe et al., 2005a; Metcalfe & Clark, 2000), compensatory responding to discrete and/or continuous perturbations (Bertenthal et al., 1997; Metcalfe et al., 2005b; Sveistrup & Woollacott, 1996), and during performance of independent walking (Clark et al., 1988; Ledebt & Bril, 2000). This instability has appeared robustly across levels of analysis in the observation that infants postural behavior is characterized by marked levels of variability and this variability leads to inappropriate responses in postural tasks. For example, in Woollacott's 'platform perturbation' studies (Foster et al., 1996; Sveistrup & Woollacott, 1996; Woollacott et al., 1987), muscular response patterns during the months surrounding onset of independent stance and locomotion were shown to be poorly scaled in terms of activation amplitude, improperly timed in terms of activation latency, and highly inconsistent in terms of the intramuscular activation sequence elicited by the perturbations. Similar results were obtained in an analogous task during the emergence

and refinement of independent sitting (Hadders-Algra et al., 1996; Hadders-Algra et al., 1997; Hadders-Algra et al., 1998) and in both standing and sitting cases, the magnitude of this variability decreased within and across participants as their posture-specific experiences increased.

Although observations of changing stability have appeared for nearly as long as postural development has been studied, explanations of the underpinnings of this change have not emerged with the same level of consistency. Per the usual route of scientific progress, however, current efforts have begun to rectify this situation. For example, a recent study (Roncesvalles et al., 2004) tested a theoretical proposition that postural development in infants is influenced by the emergence of the ability to use the musculature at the hips as a means of maintaining balance (McCollum & Leen, 1989). In this study, it was shown that although a 'hip response' to a linear perturbation could be elicited in newly walking infants, an observation that would disconfirm McCollum & Leen's (1989) proposal, more detailed assessment of muscular activity and joint torques indicated that the infants 'hip responses' were due to passive (mechanical) rather than active (muscular) factors, thus confirming the theoretical prediction. Clearly, as technology advances and investigators become increasingly skilled and innovative in its application, progressively fine details become available to facilitate the generation and testing of theoretical hypotheses regarding the nature of human postural development.

Unfortunately, even using the best available technology, it remains challenging – if not impossible – to record the quality of data that would afford complete model-based assessment of postural development. Even with extreme patience and innovative capacity, infancy researchers are ultimately constrained by the capabilities and

compliance of their participants. That is, neither increasingly precise instruments nor ever-gaining computational power will make a newly-standing or newly-walking infant able to maintain stance for any length of time greater than 30 seconds. This practical consideration has become particularly significant for studies of posture within the last decade, as human stance has been reconceived as a behavior organized across a variety of time scales (from milliseconds to minutes) and, therefore, it must be recognized that analysis of 10-30 second trials will not allow its complete characterization (Duarte & Zatsiorsky, 1999). Consequently, the field of study focused on adult postural control has been forced to accept a paradigm shift towards recording prolonged trials of quiet stance (Kiemel et al., 2002; Kiemel et al., 2006; Zatsiorsky & Duarte, 1999; Zatsiorsky & Duarte, 2000) and, of course, paradigmatic changes such as these have 'trickled down' to the community of researchers focused on early postural development.

In addition to issuing new challenges to developmental research, advancements in the models that have been formulated with respect to adult posture provide important guidance as developmental scientists progress towards mechanistic interpretations of empirical data. For example, it remains an open question as to how much developmental change in postural sway can be accounted for by the passive mechanics associated with physical growth as opposed to active, and presumably learned, recruitment of muscles. Certainly, empirical observations have indicated that both factors are influential to postural development (e.g. Ledebt et al., 1998; Roncesvalles et al., 2004), and, more to the point, the questions raised by such empirical observations can only stand to benefit from the application of established models from the adult literature. For instance, the single-segment inverted pendulum model (Winter et al., 1996; Winter et al., 1998) has

been foundational to concepts and explanations of developmental changes in a variety of both static and dynamic postural tasks (Adolph et al., 1998; Brenière & Bril, 1998; Ledebt et al., 1998; McCollum & Leen, 1989). In nearly all cases where the inverted pendulum model has been invoked, researchers have accounted for, rather than ignored, the influence of physical dynamics and further, this has led to the conclusion that active sensorimotor learning requires humans to tailor their actions to – as well as exploit the dynamics of – their own body in order to progress to advanced developmental levels of adaptive cognitive-motor behavior.

Just as adult models place important constraints on infant studies, data and concepts from developmental research have considerable potential to reciprocate. Consider, as an example, that all models describing the control processes involved in the maintenance of upright stance require the setting or determination of a variety of parameters meant to represent different physiologic subprocesses. Regardless of exactly which parameters are important to the specific model, whether muscle stiffness (Winter et al., 1998; Winter et al., 2001), PID-type feedback gains (Morasso et al., 1999; Morasso & Schieppati, 1999; Peterka, 2000) or sensory coupling constants (Dijkstra, 2000; Jeka et al., 1998), all modelers are forced to assume that there is a natural way for these parameters to be established within human physiology. Certainly, these assumptions are not without justification; if the system works in ways consistent with a given model or models, then logic would dictate that there is *something* within the human physiologic system that mimics the *function*, if not also the structure, of the essential parameters or processes depicted within that model. Yet, after efforts have advanced to the point where variety of equally plausible models are present in the literature, it becomes important that

the developmental questions are given serious consideration. In addition to conducting empirical investigations to facilitate the estimation of specific physiologic parameters such as has been done for stiffness (Loram et al., 2005; Morasso & Sanguineti, 2002; Winter et al., 1998) or control-loop gains (Fitzpatrick et al., 1996; Johansson & Magnusson, 1989), eventually, it must be asked when and how in human ontogeny these control structures and parameters were established.

The main goal of this study was to advance the understanding of the acquisition and stabilization of human posture. In particular, we used a computational approach to address developmentally-relevant questions inspired by modeling efforts and, specifically, we examined the relative contributions of physical maturation and experiential learning. Our intent was to facilitate formalized discussion of some of the specific constraints that have been logically and/or empirically implicated as influential on the development of upright postural control and, by extension, independent locomotion. In order to achieve this, we implemented a reinforcement learning approach that has recently been advocated as a powerful and relevant means of evaluating human learning and development (Berthier et al., 2005). As this method has appeared with increasing popularity in the modern literature and because it has demonstrated success in simulated depictions of learning fundamental behaviors such as standing (Borghese & Calvi, 2003; Morimoto & Doya, 2001) and reaching (Berthier, 1996; Berthier et al., 2005) it is important that the current application not only assesses the end-state behaviors produced by the model and their associated learning curves, but also examines the relative fidelity of the model with respect to how it represents real human data. Therefore, a secondary objective of this study was to qualitatively and, to the extent that it is

possible, quantitatively examine how well the reinforcement learning framework captures essential changes in human postural behavior with growth, learning and development.

Method

Shown in Figure 5.1, the developing infant was represented through the use of closed-loop structure that enacted ankle muscle torques based on motor commands that were determined as a function of the current system state. There were five main components of this model: (1) the body and it physical properties (mass, inertia, etc), (2) a neural network that determined current kinematic state based on sensory feedback regarding position and velocity, (3) an 'actor' that determined the action to take based upon the current state (aka, the controller), (4) a torque generator that included a generic representation of muscle activation dynamics and finally, (5) a 'critic' that evaluated a reward for each action and generated an error signal based on that reward that was used to drive adaptation for the sake of learning to stand.

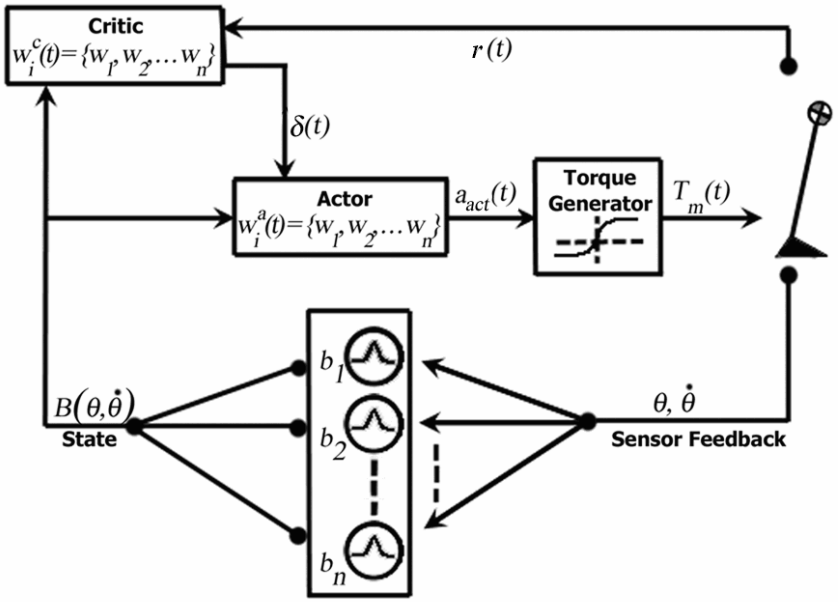


Figure 5.1. Schematic of the control system adapted for use with a reinforcement learning algorithm. All symbols and variables are explained in the text that follows.

We selected this model to represent, in a generally accepted way, the relevant physical and neural constraints on postural control and, at the same time, provide a specific computational structure for describing exploratory motor learning. Through this approach we could examine just about any realistic behavior and, with sufficient definition of the physical system and its reward, it would eventually meet the goals by means of trying to achieve a relatively non-specific task objective. In the case of the current postural model, the non-specific goal was, quite simply, 'do what you can, but try to keep yourself in the neighborhood of vertical'. In what follows, we present our model in its two main subdivisions. The first of the two subdivisions describes the selected instantiation of the body, including its physical, sensory and muscular dynamics. In the second section, the learning algorithm is presented as it applies to this physical system and the postural task.

A simple physical model of upright standing

Physical dynamics. Because this study is among the first to attempt a model-based analysis of upright postural development that explicitly includes maturational factors such as physical growth, we chose to implement a planar, single-segment inverted pendulum. The inverted pendulum has long been the standard entry point for model development in human postural control (Johansson et al., 1988; Kiemel et al., 2002; McCollum & Leen, 1989; Morasso et al., 1999; Peterka, 2000; Winter et al., 1998). This model is compelling because it provides a simple, yet sufficient representation of the physical task requirements of upright posture. While somewhat elementary in its formulation, this model provides an important foundation for extention to higher-order cases, such as inclusion of multiple segments and/or multiple axes of rotation, as

modeling efforts progress (Alexandrov et al., 2005; Borghese & Calvi, 2003; Jacobs, 1997; Kooij et al., 1999; Winter et al., 1996; Yang et al., 1990) .

The planar motion of the inverted pendulum as implemented in this study, was represented as:

$$\ddot{\theta}(t) = \frac{T_d(t) + T_m(t)}{I_{b.a}} \qquad (5.1)$$

where $\ddot{\theta}(t)$ was the angular acceleration of the body about the ankle axis in rad/s^{-2}, $T_d(t)$ and $T_m(t)$ were the disturbance and muscle torques respectively, both in units of $N \cdot m$, and $I_{b.a}$ was the moment of inertia of the body about the ankle and was calculated as the product mh^2 (m = whole-body mass in Kg and h^2 = the radius of gyration, or the squared distance between ankle and the center of mass, CM, in m). We will reserve discussion of T_m until muscle dynamics are addressed, but explain T_d here for the sake of presenting our second justification for selecting this model.

In the absence of perturbations other than those due to gravity, the disturbance torque, T_d, about the ankle was $mghsin\theta$. Mass and CM height were represented as m and h as above, g was the acceleration due to gravity (= $9.81\ m \cdot s^{-2}$) and $sin\theta$ gave the moment arm at which gravitational force acted on the pendulum[11]. When excluding the active contribution of T_m in Equation 5.1, it is easily seen that only two physical parameters, m and h are necessary to represent the passive mechanics of the single-segment system. The height of the CM reflects not only the overall height of the body, but also the relative distribution of mass among the body segments and therefore, in a single variable, h can

[11] Note that the simulated model was linearized by virtue of the small angle approximation ($sin\theta \approx \theta$), which considers the differences between $sin\theta$ and θ for small angles, such as those in the range typically observed in postural sway, to be negligible. This same linearization was applied throughout all components of the model that would otherwise have required a $sin\theta$ term.

represent important changes in body proportions that occur with physical growth and maturation. In addition to mass and height, an additional parameter representing foot length was needed to define the physical stability limits. The fact that only three anthropometric variables were essential facilitated this initial effort as compared with higher-order models by reducing the demand for anthropometric data that, as yet, do not exist in complete form[12].

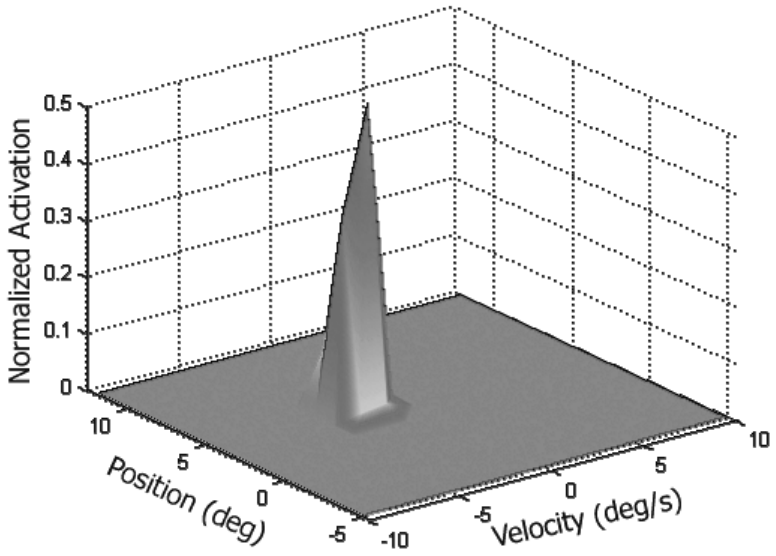


Figure 5.2 A continuous-space representation of the movement state as output from a Gaussian neural network (see text). The surface depicted here resulted from inputs $\theta = 5$ degrees and $\dot{\theta} = -2$ deg·s^{-1}. Note that the asymmetry on the position axis reflects the intrinsic asymmetry of postural sway due to the location of the ankle relative to the length of the base of support. .

Sensory-perceptual network. Figure 5.2 shows an example of the behavioral state-space as it was output to the actor and critic by a dedicated sensory-perceptual

[12] Excluding foot length, a two-segment model requires at least 6 parameters: mass, moment of inertia and radius of gyration for each segment (note that due to linked-body dynamics, moment of inertia cannot be represented as mh^2 in a multi-segment model). Because anthropometrics are not generally estimated for upper vs. lower body, information regarding 36+ parameters would be needed to determine the 6 parameters describing the two segments. Except for a few studies on various subsets of body segments (Chester & Jensen, 2005; Jensen et al., 1997; Ressler, 1977), a complete set of anthropometric data was not available for the age groups of interest at the time this study was completed.

neural network. This output was based on normalized Gaussian radial basis functions (GRBFs), which are particularly useful in systems where nonlinear input-output mappings must be established (Bugmann, 1998; Singla et al., 2007; Tresp et al., 1997). This approach is analogous to connectionist techniques involving the recruitment of 'hidden layers' of neurons that perform nonlinear transformations on input vectors (Mareschal et al., 1999; Morton & Munakata, 2005; Shultz, 2003). These hidden layers of neurons accept current state information, in our case, values of angular displacement and angular velocity, and then represent those values on a multidimensional state-space indicating a probabilisitic 'map' of current location. Such GRBF networks have proven advantageous in continuous-time, continuous space formulations of the reinforcement learning problem for typically high-dimensional balancing and force control tasks (Doya, 2000; Morimoto & Doya, 2001; Si & Wang, 2001) where discrete characterizations of the behavioral state space (such as those used in Barto et al., 1983; Borghese & Calvi, 2003) can be problematic.

With this method, the behavioral state space was represented as the summed activation of a finite number of Gaussian-shaped basis functions ('hidden layer neurons'), each defined by a center and a width, that covered all possible position-velocity combinations for the task. For the current study, the input to the GRBF network was a position-velocity pair, $x(t) = \{\theta(t), \dot{\theta}(t)\}$ (in *rad* and *rad·s*$^{-1}$, respectively) and the normalized output activation ($\tilde{b}$) of the k^{th} basis function for a given input variable at time *t* was defined as

$$\tilde{b}_k(t) = \frac{b_k(t)}{\sum_{i=1}^{N} b_k(t)} \qquad (5.2)$$

The non-normalized output of each basis function, $b_k(t)$, was defined as an exponential of the Euclidean distance between the value of the current state variable, $x(t)$, plus a small noise term, $\sigma_s n_s$ and the center of that basis function (c_k) normalized to its width (s_k).

$$b_k(t) = e^{-\left(\frac{(x(t)+\sigma_s n_s)-c_k}{s_k}\right)^2} \qquad (5.3)$$

The overall state-space then was represented as the outer product of the two vectors of basis functions calculated on the individual inputs for position and velocity, thus resulting in a matrix of cross products representing a center for each position and velocity coordinate. The *i* rows in the resulting matrix corresponded with the number of position basis functions and the *j* columns corresponded with the number of velocity basis functions. While the model used in the current study is relatively free of many assumptions regarding the system's own level of 'self-knowledge', the use of the GRBF network for parsing the behavioral state space constituted a general assumption that humans are able to perceive, or at least sense, their location within the behavioral state space – which, given multisensory integration required for such a percept, is a nontrivial task. Because the state space provided to the system ultimately defines what can be learned, it is a direct influence on the relative success in this task. As such the structure of this state space is critically important and was among the variables of interest as this investigation proceeded.

Muscle activation. As with all other aspects of the model, given the potential for a high degree of complexity hindering this initial foray into developmental modeling, our chief concern in selecting the means of representing torque generation was that it would be sufficient to afford examination of the constraints relevant to our questions without

adding unnecessary complexity to an already high-dimensional system. As such, we looked to the related modeling literature and selected a torque generator that provided an adequate balance between number of parameters and level of complexity (Morimoto & Doya, 2001). In this model, muscle torque was generated as

$$T_m(t) = u(t)T_{\max}\theta(t) + \sigma_m n_m(t) \qquad (5.4)$$

where *u(t)* was the control signal sent to the muscle, $T_{max}\theta(t)$ was the available torque when the muscle was activated (in units of $N{\cdot}m$), and $\sigma_m n_m$ represented actuator noise scaled as a proportion of maximum muscle torque (also in units of $N{\cdot}m$). For the purposes of this study T_{max} was set to *2mgh* throughout all experimental manipulations. The control signal, *u(t)*, was a nonlinear, sigmoidal function (Shultz, 2003) of the command inputs that served to constrain overall muscle torque to the limit imposed by T_{max}.

$$u(t) = \frac{2}{1 + e^{-(a_{act}(t) + a_{pass}(t))}} - 1 \qquad (5.5)$$

In using this activation function, two simplifying assumptions were made: (1) that maximum stabilizing torque could reach twice the magnitude needed to counter the disturbance torque at a given angle, as would be the case in a neutrally stable system, and (2) this value was symmetric about the ankle (although, if desired, asymmetry could be accommodated by changing the numerator and/or the constant subtracted at the end).

As shown in Equation 5.5, the control signal resulted from a summation of two inputs, here denoted as 'active' and 'passive' components. The automatic, or 'passive', component was represented as a linear servo-controller with activation output that was specified as a function of muscle stretch represented as joint angle,

$$a_{pass}(t) = -K_p\theta(t) - K_d\dot{\theta}(t) \qquad (5.6)$$

and subsequently normalized by T_{max} before being passed to the sigmoidal activation function. This component was included to represent contributions to muscle activation and force generation (whether neural or mechanical) that are generally considered automatic or passive. For this study, only the stiffness term, K_p, was non-zero when passive effects were considered and damping effects were left to be examined in another set of experiments. When set, K_p was specified as a proportion of maximum muscle torque ranging from 0 to 1 (in the simulations reported in this study, a value of $K_p = 0.4T_{max}$ was used).

The active command input was generated by a nonlinear feedback controller that represented the learned 'action policy' as discussed in the reinforcement learning literature; (Barto et al., 1983; Sutton & Barto, 1998):

$$a_{act}(t) = \sum_i \sum_j w_{ij}{}^a(t) b_{ij}(t) + \sigma_a n_a(t) \qquad (5.7)$$

Essentially, this controller calculated the active command input as a weighted function of current kinematic state, $b_{ij}(t)$, as output by the GRBF network. The weights, $w_{ij}{}^a$, specified the learned action for the current state and were adapted with each time-step as described in Equation 5.13 below. Computational noise, $\sigma_a n_a$, was included to encourage exploration as the system established its weightings through the trial-and-error learning process.

The influence and structure of noise. As with most models, noise was an important factor in obtaining data from the current simulations that were representative of human postural sway. While previous reinforcement learning models of posture-like tasks have only included one source of noise, such as in the decision process of the actor (Barto et al., 1983; Borghese & Calvi, 2003) or in the command output to the torque

generator (Morimoto & Doya, 2001), the model implemented in this study ultimately required three noise sources. As will be presented in detail the results section, the initial formulation of the model in this study only included noise at the level of the actor (the only noise coefficient that was nonzero was σ_a in Equation 5.7) and, while successful at learning to stand, this model produced behavior that was inconsistent with human postural sway. After considerable effort spent on pilot simulations, it was concluded that two more noise sources were needed, including one at the output of the torque generator (Equation 5.4) and one at the input to the sensory-perceptual (GRBF) network (Equation 5.3). The addition of noise sources in these places was considered appropriate as the human sensorimotor system is believed to act in non-deterministic ways at both the level of sensory measurements (Kiemel et al., 2002) and the motor output (Deluca, 1997).

In all cases, the noise process was a lowpass filtered signal based on a Gaussian source, $\xi(t) \approx N(0,1)$ and with a time-constant specified by τ in *s*.

$$\tau\dot{n}(t) = -n(t) + \xi(t) \qquad (5.8)$$

In the actual implementation, the three noise sources were each treated as independent, with each having its own time constant (τ_a, τ_m, τ_s; subscripts a, m and s denote actor, muscle and sensor, respectively), scaling coefficient (σ_a, σ_m, σ_s; units dependent on the associated input/output variable) and Gaussian source ($\xi_a(t)$, $\xi_m(t)$, $\xi_s(t)$).

An important difference between the noise source implemented in the actor and those implemented in the actuator and sensor network was how its magnitude scaled over time. That is, whereas σ_m and σ_s were treated as constant throughout all simulations, σ_a was time-variant in accord with the scaling rule proposed by Morimoto & Doya (2001). The scaling coefficient for actor noise, σ_a, was chosen to be adaptive in order to afford

control over the exploration-exploitation trade-off (see Ishii et al., 2002 for more in-depth discussion on this topic). That is, σ_a varied in such a way that when the system was performing poorly the actor noise would increase to encourage exploration of other possible action policies and, as performance improved, actor noise was decreased to continue to exploit the action policies that were currently working. This scaling rule used a simple min-max function:

$$\sigma_a = \sigma 0 \min[1, \quad V_0 - V(t)] \qquad (5.9)$$

The way this term operated was relatively simple. In cases where the system was performing poorly, the estimated value of the current state (*V(t)*; to be explained shortly) was lower than a preselected threshold (V_0). In such a case, the difference between V_0 and *V(t)* was greater than unity and thus, the noise coefficient was equal $\sigma 0$. Conversely, when the system was performing well, the estimated value of the current state led $V_0 - V(t)$ to be less than unity and thus the noise coefficient equaled $(V_o\text{-}V(t))\sigma 0$. As such, $\sigma 0$ placed an upper-bound on the amount of noise present in the actor and the lower-bound was determined entirely by the system performance. In practice, after the learning system had been performing long enough to achieve minimal success (e.g. not immediately toppling over), the contribution of this noise source tended to be negligible.

The learning system

As carried out in the current study, the steps in the reinforcement learning algorithm can be summarized using a convention similar to Sutton & Barto's TD_λ algorithm (Sutton & Barto, 1998) as shown in Figure 5.3.

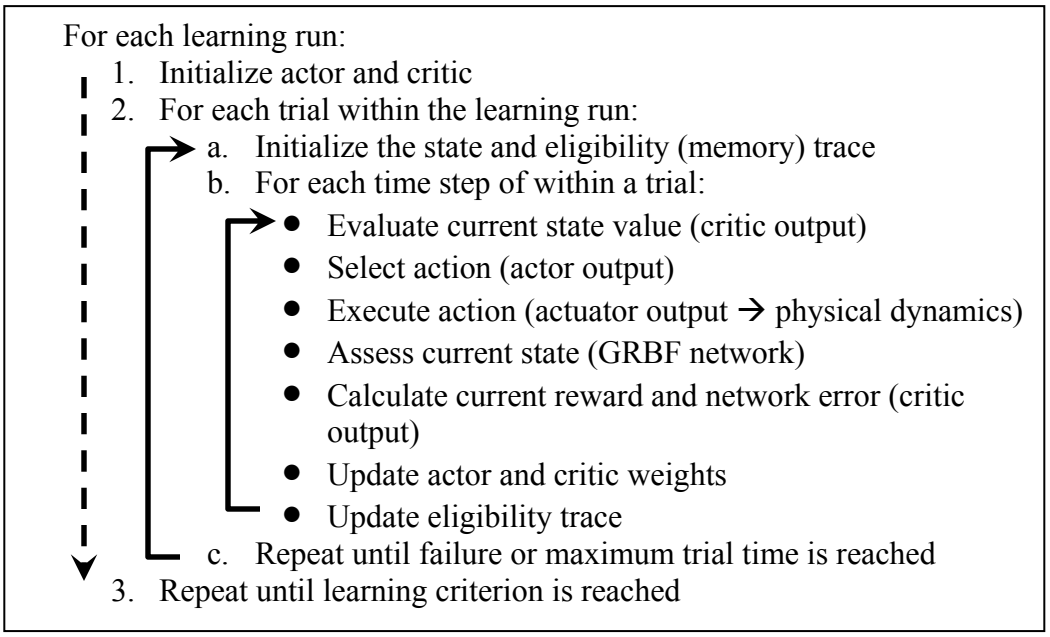


Figure 5.3 The reinforcement learning algorithm applied in this study. Dashed line indicates finite nature of a learning run, solid lines represent iterative loops.

The essence of this algorithm is in the approximation of a unitless value function that indicates the total amount of cumulative reward to be obtained when starting from any given location in state space and following the policy determined by the actor for each subsequent step through the state space (Doya, 2000; Sutton & Barto, 1998).

$$V(x(t)) = \int_{t}^{\infty} e^{-\frac{\tilde{t}-t}{\tau_d}} r(x(\tilde{t}))d\tilde{t} \qquad (5.10)$$

Assuming that the actor finds an optimal action policy appropriate for the behavioral state-space, Equation 5.10 represents the associated value function for any initial state, *x(t)* as a discounted function of increasing time in the future ($\tilde{t} - t$) and immediate reward, $r(x(\tilde{t}))$, where the future rewards are discounted by a factor of τ_d. The goal of the learner is thus to maximize the amount of cumulative reward received over time by taking the appropriate actions to navigate the areas of the state space of the greatest value. This value function was approximated by the critic in a manner analogous to Equation

5.7. That is, through action-based learning, the critic established a set of weights, w_{ij}^{c} that indicated the value of each location in state space. At a given instant in time the value, *V(t)*, of the current state was thus approximated by:

$$V(t) = \sum_i \sum_j w_{ij}^{c}(t) b_{ij}(t) \qquad (5.11)$$

In addition to this value function estimate, the critic also output network error at each time step (Equation 5.12). If the system was functioning optimally, the difference between the current reward, *r(t)*, and the time-discounted estimate of the value function, $\frac{1}{\tau_d} V(t)$, would be equal to the rate of change in the value function, $\dot{V}(t)$, resulting from the previously-enacted movement (see Doya, 2000 for derivation of optimality conditions),

$$\delta(t) = r(t) - \frac{1}{\tau_d} \mathrm{V(t)} + \dot{\mathrm{V}}(\mathrm{t}) \qquad (5.12)$$

This error was used to adjust the previously-established weightings within the actor and critic in order to improve overall performance. The weight adjustments for the actor, w_{ij}^{a}, and critic, w_{ij}^{c}, were carried out according to Equations 5.13 and 5.14 below.

$$\dot{w}_{ij}^{a}(t) = \alpha_a \delta(t)(-a_{act}(t)) b_{ij}(t) \qquad (5.13)$$

$$\dot{w}_{ij}^{p}(t) = \alpha_c \delta(t) e_{ij}(t) \qquad (5.14)$$

In each case, the amount of adjustment to the weights on a given time step was determined by the corresponding learning step-size parameter (α_a for the actor and α_c for the critic) and the direction and rate of change was given by the value of the network error, $\delta(t)$. The actor weights were directly updated as a function of current state and the

active component of the control input ($-a_{act}(t)$) that was sent to the torque generator in the previous time step. Essentially, this learning rule made a poorly-chosen course of action less likely to happen on the next time step or it made a well-chosen course of action more likely to persist.

For the critic, on the other hand, an eligibility trace was used indicate how much each weight should be updated on a given time-step.

$$\dot{e}_{ij} = -\frac{1}{\tau_e} e_{ij} + b_{ij}(t) \qquad (5.15)$$

The purpose of this eligibility trace was to account for the well-known 'credit-assignment problem'. That is, how much credit should be assigned to a particular action in a series of actions leading to a certain outcome. For example, a fall experienced during a postural task is not only due to the action taken immediately before failure, but rather, each action and state visited before the fall deserves some 'credit'. Of course, the more time that has passed following the taking of a particular action from within a particular state, the less responsibility that state-action pair has for the current state. As such, the eligibility function not only serves as a 'memory trace' or 'backup' of the action history, but also decays the eligibility of each prior state by τ_e^{-1} (a rate of s^{-1}). Thus, as shown in Equation 5.15, the critic weights were updated on each time step proportional to how long it had been since it was last visited.

Simulation procedures

Two sets of simulation experiments were carried out in this study to systematically examine several potential sources of change on overt postural behavior during its acquisition and subsequent refinement. Experiment one was conducted as a validation of the efficacy of the continuous-time, continuous-space reinforcement

learning model on which a majority of the model in this study was based (Morimoto & Doya, 2001). Because our goals differed from those of Morimoto & Doya[13], we considered it a necessary first step to ensure that the simulations would result in postural behavior that was sufficiently similar to human postural behavior. By facilitating the 'fine tuning' of the reinforcement learning model in a manner that it reliably reproduced postural behavior that was in qualitative agreement with human postural sway, the results of Experiment 1 enabled us to proceed with the simulation runs of Experiment 2. In Experiment 2, we were particularly interested in understanding the relative roles of maturation (e.g. growth) and learning (e.g. experience-based performance improvement) in postural development. Specifically, we incorporated changes in height, mass and foot length to represent overall body growth as well as the redistribution among body segments during postural development in humans in order to understand how such physical changes interact with contraints on exploratory sensorimotor *learning*.

Procedures common across experiments. The basic structure of the model, as depicted in Figure 5.1, was constant across all simulation runs. All simulations were carried out using a single-segment inverted pendulum, with physical dynamics specified as indicated in Equations 5.1 and 5.4 – 5.7. Likewise, the basic structure of the sensory (Equations, 5.2 and 5.3) and learning (Equations 5.10 – 5.15) networks were consistent across all simulations. All differential equations were integrated using Euler's method with a time-step of 0.02 s. Specific variations were introduced through manipulations of

[13] In their study, Morimoto & Doya were attempting to get a real, multi-link robot to learn to stand up from a 'supine' (or 'prone', since the robot had no head) starting position on the floor. In their approach, however, they aimed to optimize the learning algorithm in the sense of minimizing number of learning trials and amount of time needed before the task was accomplished. While it may be argued that this is similar to what the developing human infant does, the fact that Morimoto & Doya were able to get their robot to learn to stand from no prior knowledge within 20-30 minutes suggests a dissimilarity in constraints between their robotic system and the human.

either (a) noise parameters, (b) the stiffness term and/or, (c) the physical parameters of the pendulum (specifically, mass, CM height and foot length).

Within a given experiment and run, simulations followed the same basic procedure. First, based on the desired human age to be simulated, the pendulum was created using a set of 4^{th}-order regression equations describing growth in average physical parameters as a function of age in days. These regressions were based on information from a standardized database of human anthropometrics from approximately 1 month to 18 years of age (Ressler, 1977). To simulate a theoretical 'population' of individuals within the same age, a small amount of random variation (a standard deviation of 3 days) was added to the specific age input to the regression equations. In addition to variation caused by different ages, the standard amount of variability around the physical parameters within a specific age was also included by virtue of information from the same anthropometric database. As such, the distribution of physical parameters used for all simulations in this study were explicitly chosen to be representative of the average amount of variability in the human population.

With the appropriate physical parameters selected, the body description was sent along with the model and simulation parameters were to the overall simulation model. Within a simulation run, parameters were first set according to the values shown in Table 5.1, then the set of basis functions to be used with the GRBF network were calculated, the body was initialized in a pseudorandomly-chosen position offset and, finally, the simulation run proceeded until either a failure was detected, a preset maximum number of trials was reached or the system learned to balance itself according to the preset learning objective. For all simulation runs, success was defined as the system balancing itself for a

minimum of 20 seconds on 5/5 or 8/10 consecutive trials (in all cases, simulations achieved the 5/5 criterion on ~75% of successful runs and thus, achieved the 8/10 criterion ~25% of the time); failure was always defined as the moment when the horizontal position of the CM left the area described by the forward and rear limits of the foot.

In addition to defining when a failure occurred, the size of the foot also factored into the calculation of the centers and widths of the basis functions within the GRBF network as well as calculation of the distribution of random position offsets for trial initialization. Because the foot is intrinsically asymmetric, this also meant that failure, the network of basis functions and the distribution of position offsets were also intrinsically asymmetric. In particular, all three of these relied upon definition of the forward and rearward limits as the inverse sine of the appropriate horizontal distance (either ankle-heel or ankle-toes) divided by the height of the CM. To account for asymmetry, the maximum forward horizontal motion was set to 70% of the foot length and thus, the maximum rearward horizontal motion was set to 30% of the foot length. As such, both linear and angular displacements were set such that upright vertical corresponded with a value of zero (see also Figure 5.2.).

For the GRBF network, 35 basis functions were linearly spaced in between the maximum forward and rearward angular displacement[14]. Lacking a clear physical boundary on the upper limit of velocity, however, setting the GRBF centers involved a slightly different logical (and partially empirical) process. First, the undamped natural

[14] actually, for computational reasons, a small 'margin' of 1 cm was added to the maximum forward and rearward horizontal displacement before the maximum angular displacements were determined. Thus the edges of the GRBF network were always larger than the actual physically permissible limits by a factor of *(0.01/h) m*, where *h* = height of the CM as above.

frequency (ω_0) of the pendulum was calculated as described in accord with (Winter et al., 1998), assuming zero stiffness; $\omega_0 = \sqrt{(mgh)/I_{b.a}}$. This frequency was then divided into twice the maximum amplitude (θ_{max}) as determined based on foot size to yield an estimate of the maximum average velocity (v_{max}) of motion across once entire cycle of physically-permissible sway displacement. Because initial pilot simulations indicated that this yielded a set of velocity basis functions that was too restrictive to account for the actual velocities observed in the simulation, we ultimately defined 35 basis functions that were linearly spaced between $\pm 2v_{max}$. As such, the overall sensory network involved 35 × 35 (position × velocity) bin centers spread throughout the entire behavioral state space, and the widths of the basis functions within each dimension were specified as half of the average distance between successive bin centers (Bugmann, 1998).

Table 5.1 Summary of model parameters implemented in Experiments 1 and 2

	Experiment 1				Experiment 2
Parameter	*Control, Nonstiff*	*Control, Stiff*	*Noisy, Nonstiff*	*Noisy, Stiff*	*Noisy, Stiff*
T_{max}	$2mgh$	$2mgh$	$2mgh$	$2mgh$	$2mgh$
K_p	0	$.4T_{max}$	0	$.4T_{max}$	$.4T_{max}$
K_d	0	0	0	0	0
τ_a	0.1	0.1	0.1	0.1	0.1
τ_s	0.8	0.8	0.8	0.8	0.8
τ_m	0.1	0.1	0.1	0.1	0.1
$\sigma 0$	0.1	0.1	0.1	0.1	0.1
σ_a	Equation 5.9	Equation 5.9	Equation 5.9	Equation 5.9	Equation 5.9
σ_s	0	0	$0.01\theta_{max}$	$0.01\theta_{max}$	$0.01\theta_{max}$
σ_m	0	0	$0.015T_{max}$	$0.015T_{max}$	$0.015T_{max}$
α_a	0.02	0.02	0.02	0.02	0.02
α_c	0.02	0.02	0.02	0.02	0.02
τ_e	0.1	0.1	0.1	0.1	0.1
τ_d	0.5	0.5	0.5	0.5	0.5

The immediate reward used in calculating network error (*r(t)* in Equation 5.12) was determined as a nonlinear function of the behavioral state-space. Maximum reinforcement (*r(t) = 0*) was given to the state $\theta = \dot{\theta} = 0$, a small punishment was given to position/velocity combinations in the neighborhood of vertical (*-0.1* $\leq$ *r(t) < 0*), larger punishment (*r(t) = -1*) to all position/velocity combinations outside of a pre-selected range but still within the behavioral state-space and finally, maximum punishment (*r(t) = -1.5*) was assigned to a failure. Explicitly,

$$r(t) = \begin{cases} e^{-r_{pos}^2(t) + r_{vel}^2(t)} - 1; & \text{when successful} \\ -1.5; & \text{upon failure} \end{cases} \tag{5.16}$$

where,

$$r_{pos}(t) = \frac{\theta(t)}{\sqrt{\frac{(0.1 \cdot \theta_{\max})^2}{\ln(1-0.9)}}}$$

and

$$r_{vel}(t) = \frac{\dot{\theta}(t)}{\sqrt{\frac{(0.1 \cdot 2v_{\max})^2}{\ln(1-0.9)}}}$$

Equation 5.16 specifies immediate reward as a small Gaussian shaped curve within the range of $\pm$ *0.1*$\cdot\theta_{max}$ for position and $\pm$ *0.1*$\cdot$*2*v_{max} for velocity wherein the magnitude of reinforcement gradually drops from 100% to 90% of maximum, then is at a level of -1 for all positions/velocities outside of this range and is -1.5 upon failure. This reward disproportionately encourages maintenance of all position/velocity combinations within $\pm$ 10% of the maximum allowable range surrounding the absolute center at $\theta = \dot{\theta} = 0$, where the position/velocity range was defined in the same manner as it was for the GRBF

network. As with the use of the GRBF network, the way in which we structured the reward function constitutes an assumption; that is, for this set of experiments, we assumed that the system is biased to remain near vertical when learning the task of upright standing and actively tries to prevent large deviations from vertical.

Specific experimental procedures. Table 5.1 presents a summary of all parameters implemented in the different experiments of this study. Experiment 1 was designed as a two-way comparison of models focused on (a) which types of noise and (b) whether stiffness would have an impact on learning postural sway. Specifically, this experiment compared a model that was representative of the types of parameter schemes already published in the reinforcement learning literature, that which we called the 'Control model', with a model that we determined through pilot testing to produce behavior more closely approximating human postural sway, that which we called the 'Full Noise' model. In the Control model, only 'decision noise' was included within the actor and all sensory and actuator processes were assumed to be deterministic based on the inputs. In the Full Noise model, however, all of the major processes were conceived of having some level of noise associated with the specific information represented. That is, in addition to the decision noise implemented in the actor, the Full Noise model included a stochastic source at the output of the actuator that was scaled to the magnitude of torque output (representing a noisy response to a motor command) and, likewise, a noise source at the input to the GRBF network that was scaled to the detectable range of postural sway (representing noisy sensory measurements). In addition to the comparison of noise, some of the conclusions from our previous work (Metcalfe et al., 2005a) have led us to consider the relative importance of a parameter representing 'passive' or 'automatic'

components of the muscular contributions to postural sway – and, as such, we chose compare models that either did or did not contain a stiffness term (K_p).

An important element of Experiment 1 was the establishment of the appropriate model for examining the influence of changing physical parameters on postural development. That is, the model identified in Experiment 1 as most closely representing human postural sway (the Full Noise, Stiff model) was to be the only one examined across changes in height in Experiment 2. In Experiment 2, the same model was replicated 10 times on each of 7 different ages representing a range of human postural abilities as well as the full range of physical development. Specifically, the Full Noise model was examined at discrete age steps of 6 months, 9 months and 1, 2, 5, 10 and 18 years in order to represent a full range of physical growth between immaturity and maturity. In each case, the model was initialized with no prior knowledge and thus, had to learn to stand 'from scratch'. Learning rates as well as end-state postural behaviors were examined as a function of increasing age as well as body size.

Results

Experiment 1: Validation of Model Structure

As will be made evident throughout the following presentation, the overall result of this first experiment was in strong support of characterizing human postural learning using the Full Noise, Stiff model. Through a variety of measures of learning and postural sway, the following data indicated that reinforcement learning models of human posture need to contain considerably more noise than has been used in past and further, that such models should indeed contain passive, or automatic, influences over muscle activation if they are to represent realistic human postural sway behavior.

Before proceeding with the analysis of results from this experiment, we first need a brief discussion of the population that was simulated. In order to generate a realistic set of data to compare with what is already known about human posture, we chose to carry out this first experiment through simulations of adult humans. To do this, we used 4^{th}-order regression equations to define physical characteristics for n=50 unique participants for each model (N = 200 total). To validate against the chance of one or more of the populations having differed from the others, a 2 (Noise: Control, Full Noise) × 2 (Stiffness: NonStiff, Stiff) factorial ANOVA was run on each of the age and physical parameters. This analysis verified that the populations, shown in Table 5.2, were simulated as intended; that is, there were no significant differences or interactions (all $p > 0.1$).

Table 5.2 Characteristics of simulated populations (n = 50) for each model examined in Experiment 1.

	Control Model	Stiff Control Model	Noisy Model	Stiff Noisy Model
Age (days)	6574.28 (3.19)	6574.59 (2.53)	6574.30 (3.11)	6574.83 (2.45)
Age (years)	17.999 (0.009)	18.000 (0.007)	17.999 (0.009)	18.001 (0.007)
Mass (Kg)	65.48 (11.59)	65.74 (12.68)	64.49 (12.83)	63.66 (12.07)
Height (m)	0.909 (0.043)	0.900 (0.061)	0.900 (0.057)	0.906 (0.051)
Foot Length (m)	0.253 (0.017)	0.250 (0.018)	0.253 (0.021)	0.253 (0.018)
Ankle Height (m)	0.068 (0.010)	0.067 (0.010)	0.065 (0.009)	0.065 (0.008)

Notes: Only Age (days) was included in the statistical analysis, Age (years) is shown only as a convenience for the reader.

Learning Measures. Overall, a 2 (Noise: Control, Full) × 2 (Stiffness: NonStiff, Stiff) factorial ANOVA revealed significant differences for Noise, but not Stiffness, on the rate of learning to stand up in this fixed body-size learning model. Shown in Table 5.3, all measures of overall learning rate showed that the full model containing sensory, actuator and decision noise took longer to learn than that containing only decision noise; certainly a finding that was not unexpected. Specifically, the mean trial number of the first success (Trial of First Success: $F_{1, 196} = 13.56, p < 0.0003$), mean number of trials to reach the learning criterion (Trials to Criterion: $F_{1, 196} = 20.55, p < 0.0001$), and the mean cumulative amount of time prior to the first success (Pre-Success Time: $F_{1, 196} = 27.18, p < 0.0001$) were all highly significant for condition but showed no effects for Stiffness and no interactions.

Table 5.3. Measures of learning rate indicating a significant effect for Noise, but not Stiffness (means with standard deviations in parenthesis).

Variable	Control Noise Only	Full Noise Model
Trial of First Success	359.61 (69.82)	399.75 (83.83)
Trials to Criterion	409.40 (90.85)	474.20 (111.00)
Time to First Success	400.98 (69.82)	460.30 (89.78)

Notes: Decimals for trial numbers indicate averages that produced significant effects in the ANOVA, however, no 'partial trials' were actually defined or recorded as such. Time to first success is listed in seconds.

The learning effects, as well as the marked differences in learning between the models, were more clearly revealed by fitted learning curves. Because preliminary investigation suggested that the function underlying the shape of the learning curves may have varied with model structure, all learning curves were fit with both an exponential

and a step-function, and these two fits were compared with one another across the four models. For the exponential curve, the equation $\hat{y} = b_0 + b_1 e^{b_2 N}$ was fit using the nonlinear Nelder-Mead algorithm (function fminsearch.m in Matlab). For these exponential learning curves, $\hat{y}$ was trial duration and *N* was trial number. As with the exponential function, three parameters were used for the step function; these included the trial number of the step, the median trial duration before and the median trial duration after the step. In the case of the step function, an iterative fitting procedure was used. For each observed learning curve, all possible step functions described by the three parameters were created, the residual error between each possible step function and the observed learning curve was determined, and the step function that produced the lowest residual error was selected as the best fit function. Following the fitting, the exponential and step functions were compared with one another by means of a fit-assessment measure known as the Bayesian Information Criterion (Gagne & Dayton, 2002; Schwarz, 1978), which assesses both the structure (e.g. takes into account the number of parameters) as well as the quality of the fit (e.g. size of the residuals).

The standard approach for using the BIC is to select the fit that produces the lowest value. As such, the exponential and step functions were compared in a pairwise manner by subtracting the BIC that was calculated on the step function from that calculated on the corresponding exponential, thus creating a variable that we call BIC_{diff} ($BIC_{diff} = BIC_{exp} - BIC_{step}$). Because the fit with the lowest value is considered the 'preferred' fit, cases where BIC_{diff} was negative indicated a preference for the exponential function and, concomitantly, preferences for the step function were indicated by a positive BIC_{diff}.

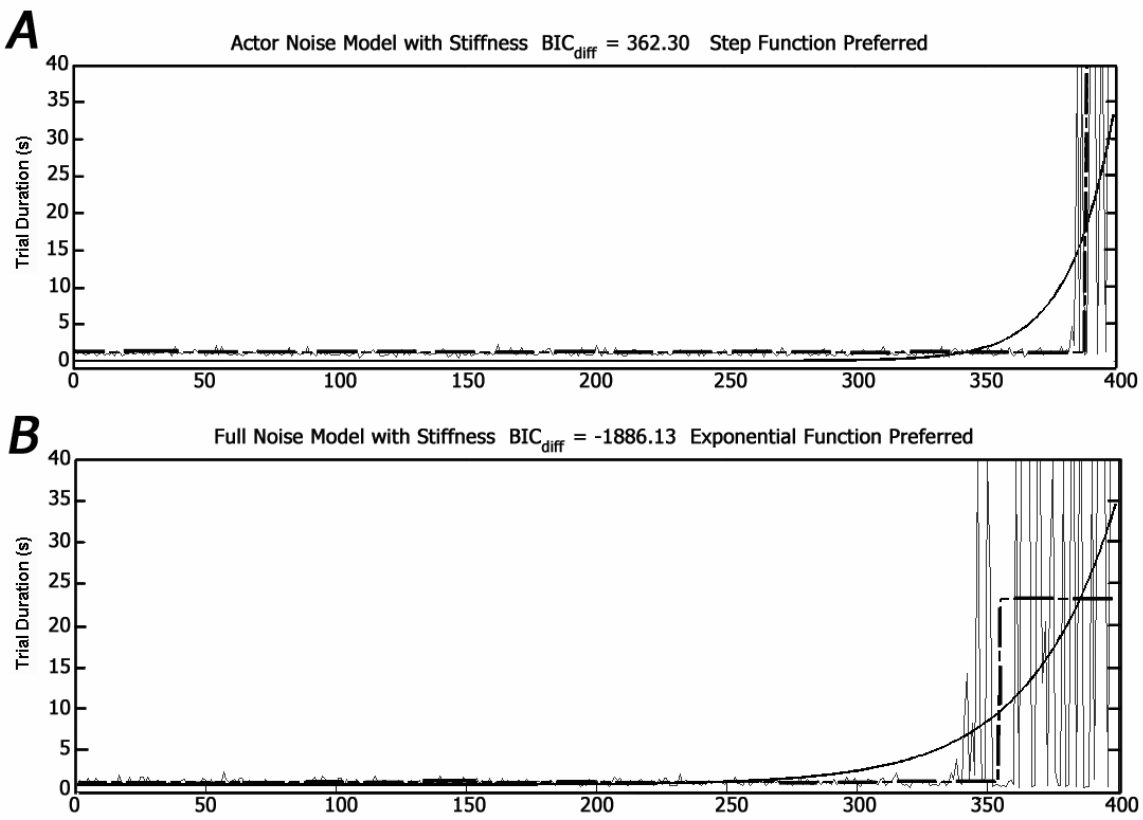


Figure 5.4. Exemplar learning curves with step and exponential function fits for simulated stiff models with (A) actor noise only and (B) actor, actuator and sensory noise. Dash-dot line represents the best-fit step function and solid dark line represents the best fit exponential.

The BIC_{diff} values were then statistically analyzed using the same 2 × 2 ANOVA that was applied to all other measures in this first experiment. This ANOVA revealed a significant Noise × Stiffness interaction ($F_{1,196} = 10.01$, $p < 0.002$) such that the two models without stiffness had values of BIC_{diff} that revealed no clear preference for a fit, but stiff models with actor noise only were best fit with a step function and stiff models with full noise were best fit with an exponential function. Figure 5.4 provides exemplar learning curves for each of these two conditions (Note that the exemplars were selected for simulation runs achieved the learning objective in an equal number of trials).

Finally, this generalized difference in 'shape' of learning was revealed in two statistical interactions regarding the relative amount of experience acquired by each

model while learning to stand. That is, owing to the differential rate and characteristic shape of learning, the full noise model tended to accumulate more overall experience than did the model that only had noise in the actor. Specifically, while the full noise model tended to arrive at both its first success and the overall learning criterion later than did the control model, examination of the time *between* the first success and achievement of final learning objective revealed a 'hidden advantage' for the full noise model in terms of cumulative experience. Both the data in Table 5.3 and the curves depicted in Figure 5.4 depict this finding nicely. Supporting this inference were two significant interactions as depicted in Figure 5.5. For both the total number of successful trials experienced (Figure 5.5a) and for the total amount of time spent standing throughout learning (Figure 5.5b), the 2 × 2 ANOVA revealed a significant Noise x Stiffness interaction (Number of successes: $F_{1, 196} = 5.56, p < 0.02$; Total standing time: $F_{1, 196} = 5.29, p < 0.03$). In both cases, this interaction indicates that for the stiff model only, there was a general increase in *experience during learning* when noise was added to the model.

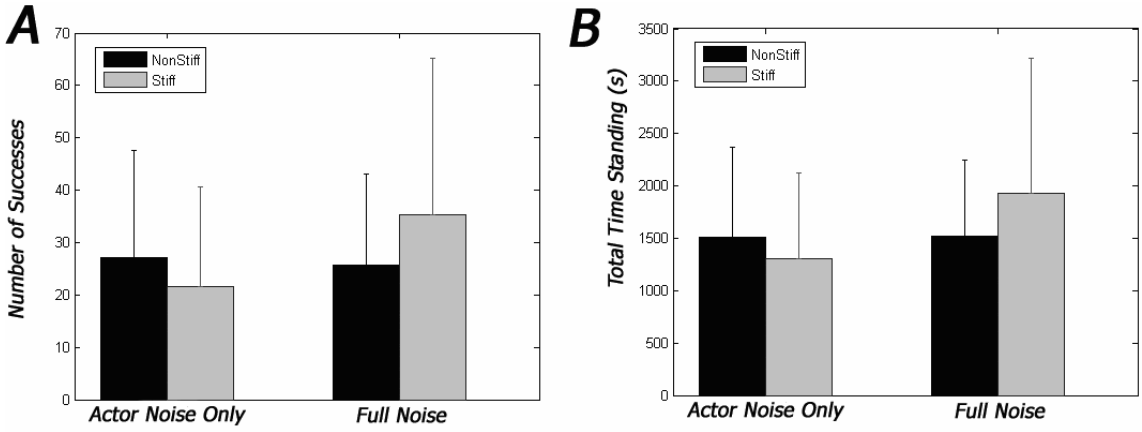


Figure 5.5. The interaction of Noise and Stiffness as detected by (A) total number of successes and (B) total amount of time spent standing during learning. Errorbars represent standard deviations.

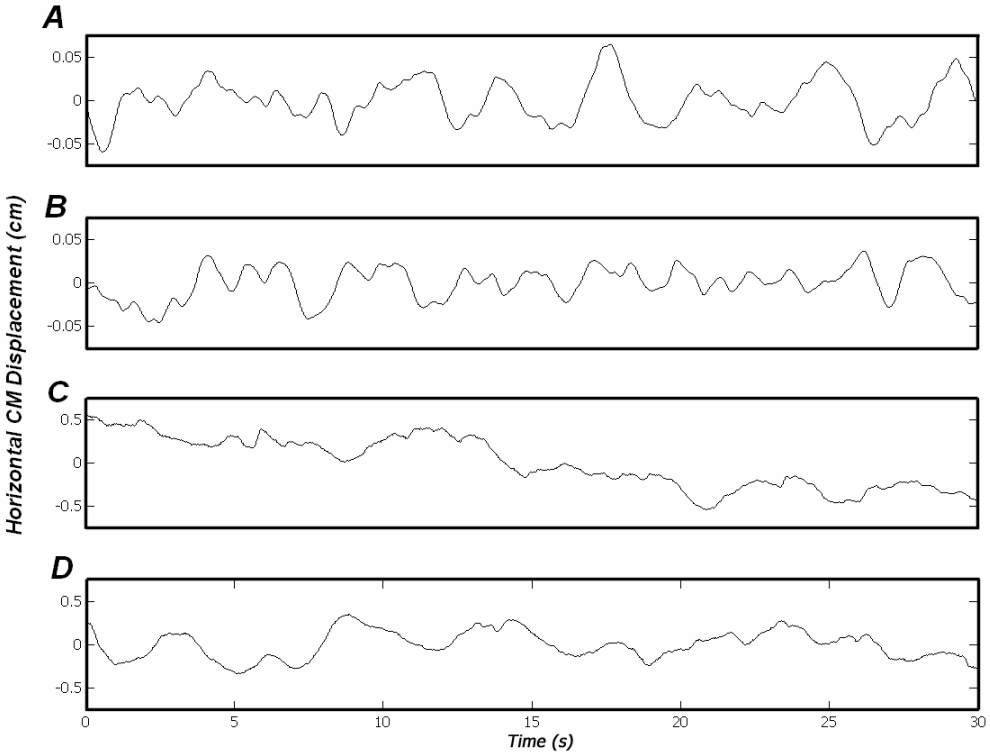


Figure 5.6. Exemplar time series of postural sway for one trial of each simulated model of an 18 year old adult; (A) Control, Nonstiff, (B) Control, Stiff, (C) Full Noise, NonStiff, (D) Full Noise, Stiff. Note that the vertical scale of the top two panels is a full order of magnitude smaller than that of the bottom two panels.

Characteristics of postural sway. While assessment of the characteristics of learning have informed our understanding of the nature of the interaction between the reinforcement learning algorithm and a posture-like system, it is essential that we now assess the nature of *what* was learned. Figure 5.6 provides exemplar time-series for each model depicting horizontal center of mass (CM) displacements during the middle 30 seconds of one trial at the end of learning when the system successfully remained upright for a full 40 seconds. Only the middle 30 seconds are shown to represent the steady-state behavior that was learned, excluding the initial transient due to the randomly imposed initial position offset. The immediate impression is that, qualitatively, each of these time-series appears as human postural sway would appear. That is, each time-series seems to

be an irregular oscillatory pattern representing the combination of multiple frequencies. However, closer inspection reveals some important differences. For example, in comparing the behavior learned by the Control model (actor noise only; top two panels), we see that the scale of excursions is an order of magnitude smaller than those produced by the full noise model. Further, a more trained eye might note that the oscillations within the two bottom panels appear to be more gradual; that is, characterized by somewhat slower back-and-forth motion. As will be seen shortly, these qualitative observations were supported with considerable statistical evidence. Analysis with multiple 2 (Noise) × 2 (Stiffness) factorial ANOVAs revealed that dramatically different sway behaviors were produced by the four models simulated in this experiment (all omnibus $p < 0.0001$).

To control for issues associated with edge-effects at the beginning and end of each trial, we only analyzed postural sway for the last five trials of each simulation run where the system successfully balanced for 40 seconds. Specifically, we excluded the first and last 5 seconds of data for each 40-second trial, subtracted the mean from the remaining 30 s segment and then calculated all one-dimensional amplitude, velocity and frequency measures as initially developed by Prieto et al (1996) and used in our earlier work (Chen et al, 2007a). Therefore, all descriptive measures were computed on an equal amount of sway data for each simulation run and condition using a constant frequency resolution of 1/15 s = 0.067 Hz and a range of 0 – 25 Hz over which the sway behavior could be assessed. For calculation of measures associated with spectral power, the dc component of the signal (0 – 0.067 Hz) was excluded. Unlike Prieto et al (1996), who ignored all frequencies below 0.1 Hz, we chose to include the lowest frequencies beyond

the dc component in our analyses as it is now known that the majority of human postural sway variance is accounted for at very low frequencies.

Table 5.4. Measures of postural sway indicating a significant effect for Noise, but not Stiffness (means with standard deviations in parenthesis).

Model	MDIST (cm)	RDIST (cm)	POWER (cm^2)
Control, NonStiff	0.028 (0.016)	0.037 (0.021)	0.051 (0.080)
Control, Stiff	0.031 (0.019)	0.042 (0.026)	0.051 (0.070)
Full Noise, NonStiff	0.212 (0.046)	0.262 (0.056)	1.095 (0.892)
Full Noise, Stiff	0.208 (0.032)	0.257 (0.038)	1.001 (0.674)
Human sway	0.242 (0.097)	0.295 (0.108)	0.88 (0.051)

Notes: MDIST = mean absolute distance from center; RDIST = r.m.s. distance from center; POWER = total power summed across frequency components ranging from 0.06 to 5 Hz. Human sway data are based on (Prieto et al., 1996), note the reduced power as compared with the Full Noise models assessed in this study.

Sway amplitude. Shown in Table 5.4 is perhaps the most compelling result from this first experiment – noise is required to produce postural sway of a physiologically-realistic magnitude. That is, in general after learning, the two Control models produced postural sway that was an order of magnitude smaller than the sway produced by the Full Noise model. Without noise, the learner ultimately was able to remain standing with sway that was only observable on a scale of a few tenths of a millimeter. This observation was statistically verified across all measures that were influenced by the amplitude of postural sway excursions, including MDIST ($F_{1, 199} = 1642.49, p < 0.0001$), RDIST ($F_{1, 199} = 1642.49, p < 0.0001$), and TOTAL SPECTRAL POWER ($F_{1, 199} = 1642.49, p < 0.0001$). Of further importance, comparison of values from the two Full Noise models

with measures of human postural sway (Prieto et al., 1996) suggests that the amplitudes observed in the Full Noise models were most consistent with magnitude of postural sway observed in the human adult. As an important aside, the fact that our observed POWER was larger than what was reported by Prieto and colleagues is a by-product of our inclusion of lower frequency components in the calculation of frequency-domain measures. Moreover, that our measures reflected an increase in POWER by including these lower components is further validation that our final model produced postural sway similar to that of the adult human; that is, we observed significant postural variance accounted for at the lower portion of the frequency spectrum.

Sway rate. In addition to the main effects for sway amplitude observed across levels of noise in the models, there were three significant Noise × Stiffness interactions. Shown in Figure 5.7, all of significant interactions were seen in the rate-related, as opposed to the amplitude-related, aspects of postural sway. Examining the mean velocity (MVELO), mean centroidal frequency (CFREQ) and the dispersion of the sway frequency distribution (FREQDisp), it was shown that stiffness was only influential over the learned postural sway in the Full Noise models. This interaction, indicated that the contribution of stiffness within a noisy model of human postural sway is to modify rate properties and, in particular, increasing stiffness is associated with increases in the observed velocity and frequency content of the sway behavior that is learned.

Experiment 2: Interaction of maturation and experience

With the lessons learned from the first Experiment, we applied the model that most closely represented human postural behavior to a comparison of that same model as it learned under different physical constraints. Specifically, based on the previous

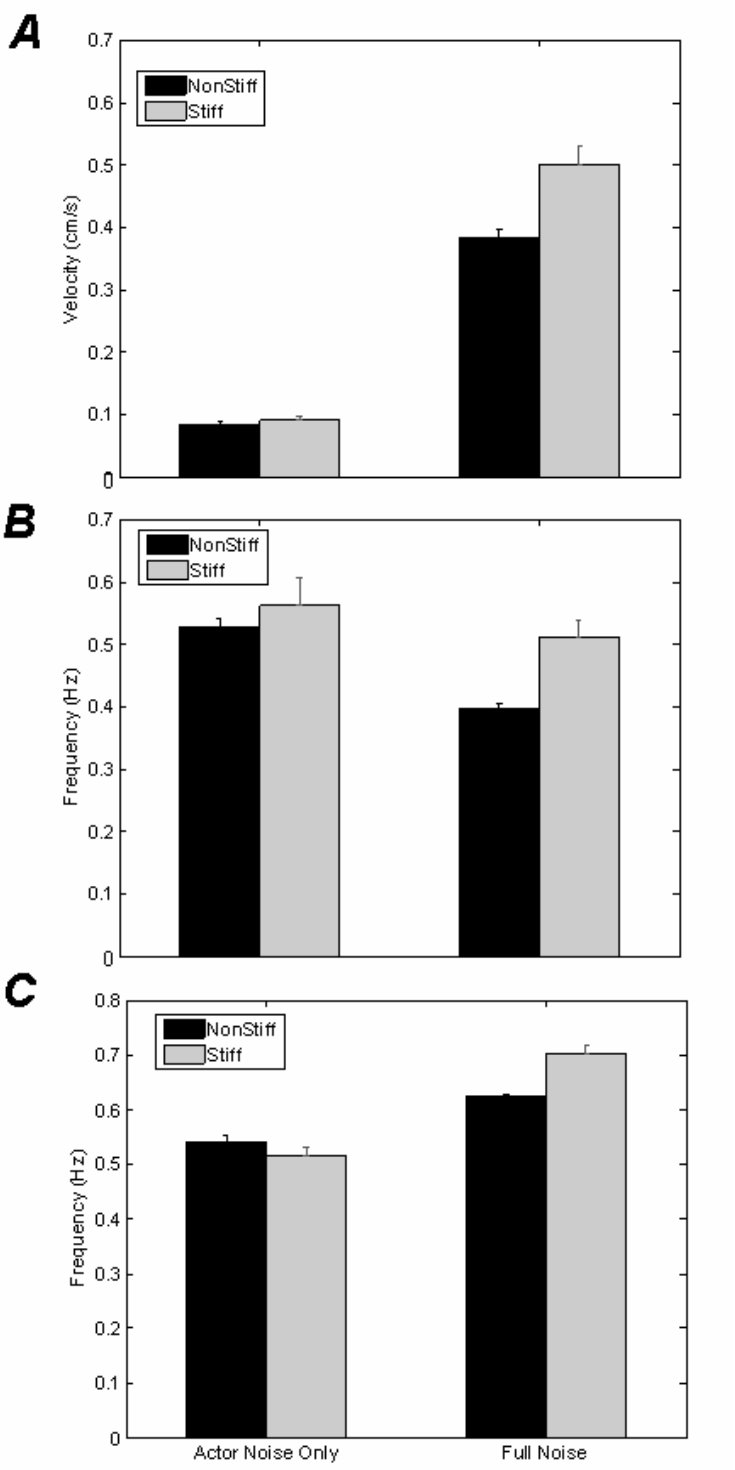


Figure 5.7 Noise × Stiffness interaction for rate properties of simulated sway including (A) mean velocity, (B) centroidal frequency and (C) frequency dispersion.

analysis, we considered either of the Full Noise models to closely depict the statistical properties of human postural sway as have been observed in adults. Owing to the more gradual learning curve of the Full Noise, Stiff model as compared with all others, we selected it as the most representative of a *developing* human postural system. In this experiment, we simulated 10 individuals at each of 7 different ages ranging from just prior to true human standing onset (6 months) until full adult maturity (18 years). In what follows we show that, while the nature of the interaction between learning and 'growth' as implemented in this set of simulations was inconsistent with human growth (in other words, the models at each simulated age had to start from zero initial success), the behavioral changes observed with increased age were consistent with what has been observed in empirical studies of human postural development.

Age and learning rate. Shown in Figure 5.8, there was a strong relationship between overall rate of progress towards successful standing and age of the simulated learner. Specifically, applying a linear mixed-model regression to measures of learning rate from each set of simulations (n = 10 at each age), we noted a considerable reduction in time that was necessary to learn to stand as a function of increased age. For example, Figure 5.8a shows a clear reduction in the number of trials required to reach the learning criterion from approximately 1000 trials in a model simulated with the physical body of a 6 month-old to approximately 500 trials in a model simulated with the physical body of an 18 year-old. This observation was borne out statistically, with a significant rate of decrease equal to -0.076 ± 0.01 trials per day of increased age ($F_{1, 66} = 57.36$, $p < 0.0001$).

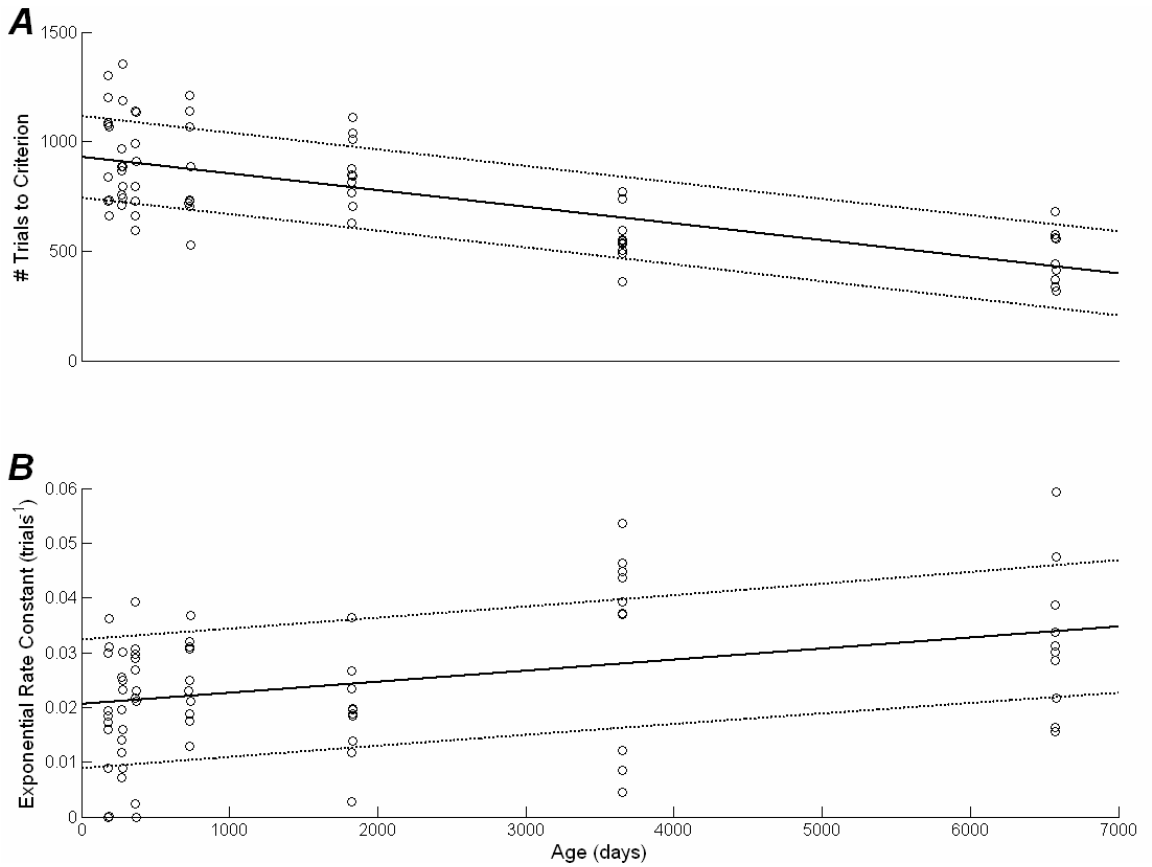


Figure 5.8. Significant regression effects for learning rate across increasing simulated age of stance acquisition. (A) Shows the number of trials required to reach the learning criterion and (B) shows the rate constant from an exponential fit to each learning curve across simulated ages. Each open data point represents the value obtained from one simulation run, the solid lines indicate a least-squares fit of the regression function and the dashed lines indicate the 95% confidence interval on the regression estimates.

Because of our observations in Experiment 1, which suggested a gradual course of learning with a Full Noise, Stiff model, we fit the learning curves from each of the 10 simulation runs at each age with an exponential function to directly examine the average continuous learning rate. Figure 5.8b displays that there was a significant increase in the learning rate concomitant with increased simulated age of acquisition ($F_{1, 59} = 12.50$, $p < 0.001$). This measure, specifically the rate constant of the exponential learning curves, suggested that, as the simulated age increased, the system learned how to maintain an upright position more rapidly.

Growth and learning to stand. Because of the considerable difference in rate of acquisition across increasing simulated age, it was imperative to examine *why* age should have been associated with such a dramatic effect on learning rate. That is, at least from the perspective of the learning algorithm itself, the age of the system should not have mattered because there was no direct representation of it within either the physical or learning systems. Instead, it seems reasonable to examine the influence of that which changed with increased simulated age – the physical parameters of the simulated body.

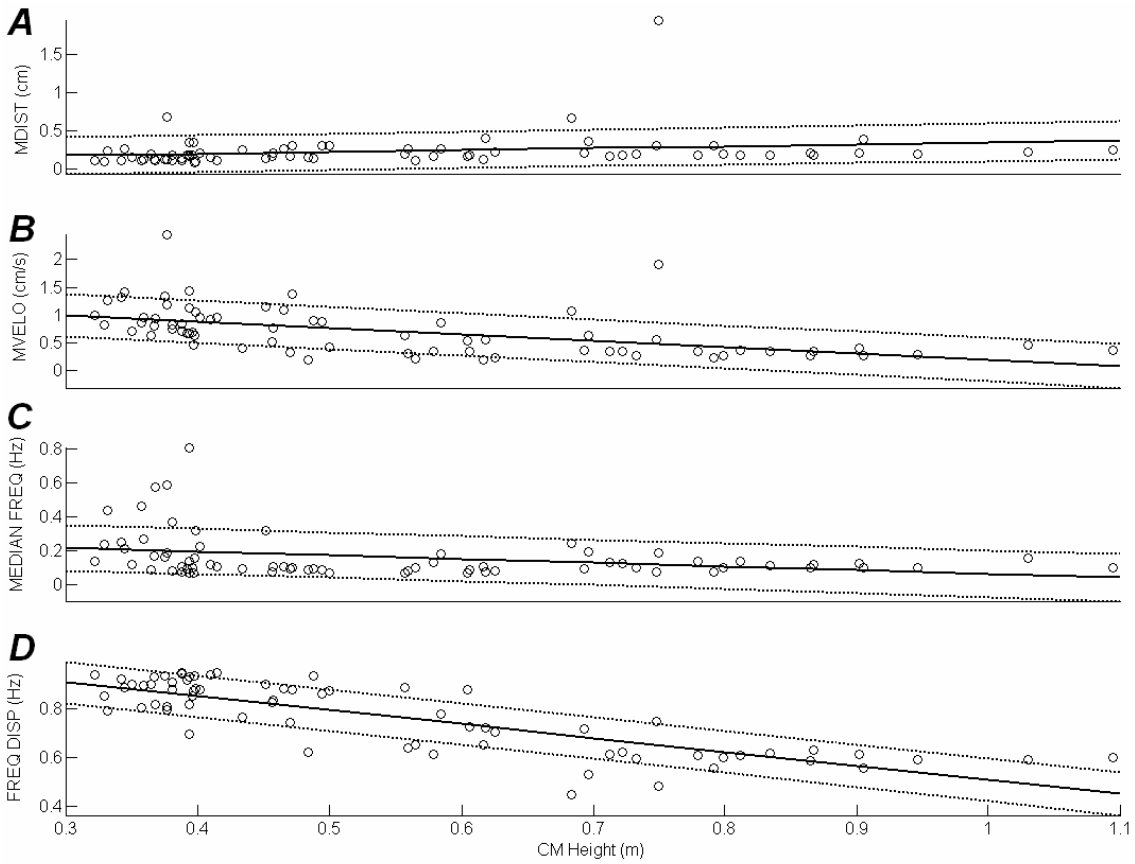


Figure 5.9. Significant regression effects for changing properties of learned postural sway across CM height. From top to bottom, the measures displayed are (A) mean distance from center position, (B) mean sway velocity, (C) frequency at which 50% of the power in the sway time series is concentrated and (D) the dispersion of the frequency power spectrum. Open circles represent the average from all 40 second trials of sway from a single learning run; solid lines represent weighted linear regression fits and dashed lines represent the 95% confidence limits on the observed regressions.

To assess the relationship between postural learning and physical size, we calculated mean measures of sway for every 40 second trial during a single learning run for each simulated age. Because of the stochastic nature of these simulations, there was a variable number of 40-second trials for each simulation run. Therefore, the means were examined using a linear mixed-model regression with the number of observed 40 second trials as a weighting factor for each mean. As can be seen in Figure 5.9a, there was a significant linear relationship between center of mass height and postural sway for every calculated measure. Of the variables examined, the only increase was observed in the mean absolute distance from upright center, MDIST, which increased at a rate of 0.12 $\pm$ 0.05 cm per 1 m increase in CM height ($F_{1,\ 13.1} = 6.63,\ p < 0.03$). All rate-related measures on the other hand, depicted in Figure 5.9b – Figure 5.9d, revealed a significant decrease with increased height of the CM. In particular, there was an observed -1.14 $\pm$ .22 cm/s per meter reduction in mean sway velocity (MVELO: $F_{1,\ 59.6} = 26.52,\ p < 0.001$), a decrease of -0.22 $\pm$0.08 Hz per meter decrease in median frequency (MEDIAN FREQ: $F_{1,\ 59.6} = 7.76,\ p < 0.01$) and a -0.58 $\pm$0.05 Hz per meter decrease in the dispersion within the postural sway frequency spectrum (FREQ DISP: $F_{1,\ 68} = 129,\ p < 0.0001$) as center of mass height increased.

Qualitative analysis of learning. As a final part of this analysis, we chose to examine in greater detail the question of what was learned. That is, as we have seen, there was a significant increase in the speed of learning as the simulated age of acquisition increased. Because of the lack of direct representation of age as a variable in our physical and learning model, we then looked to an age-associated variable that might explain this observation. In so doing, we found considerable evidence that learning to

maintain postural sway was influenced considerably by the changing height of the center of mass, as would be predicted by any physical model of an inverted pendulum. Yet, it remains unclear exactly why the change in the center of mass would have such a profound effect on the overall learning rate. After all, other parameters of this model, such as magnitude of maximum torque and amount of stiffness were held constant across age in the sense that they were always calculated based on the physical parameters of the body. This effectively 'normalized' across simulations by means of ensuring that each individual system was provided the torques needed to balance and thus, each system needed only to learn when and how much torque to apply based on current state.

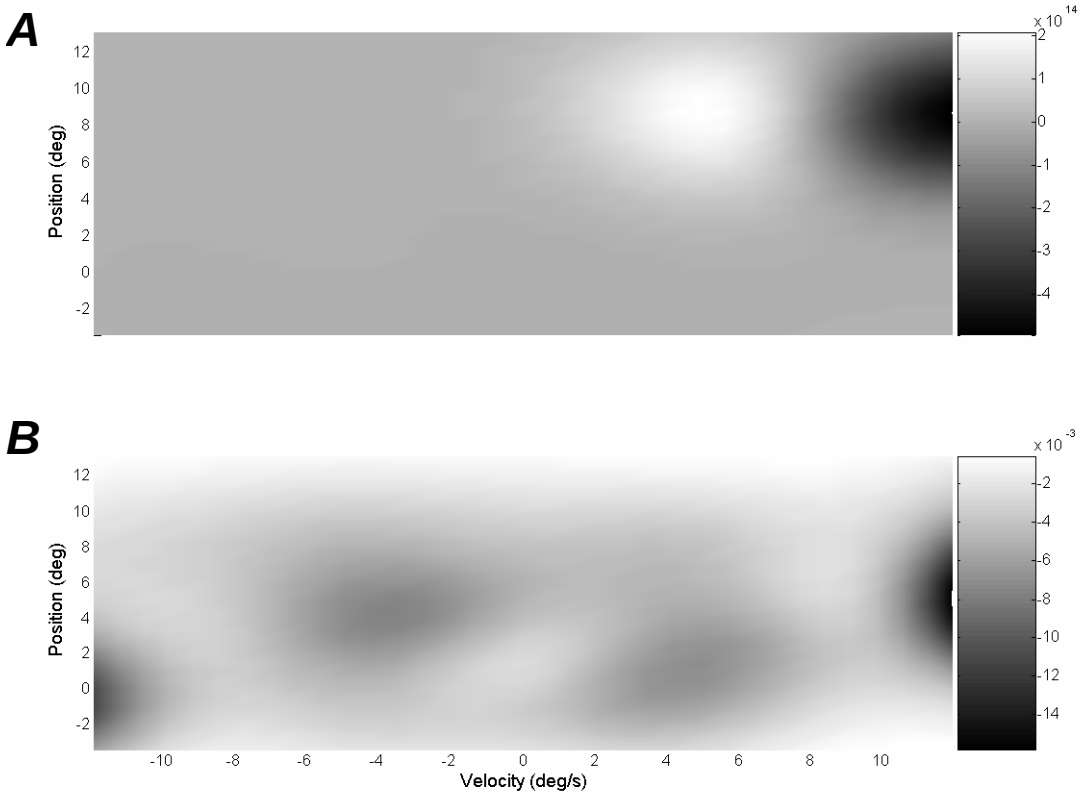


Figure 5.10. Final weights determined at the end of learning for a simulated 9 month old, by the (A) actor and (B) critic. Velocity is shown on the horizontal and position on the vertical axes; darker shading indicates increasingly negative weight values.

As such, prior to drawing any final conclusions, we performed a qualitative analysis on the specifics of what the learning systems came to 'understand' about the task of remaining upright. That is, how did age and changing physical dynamics influence what the system learned about the task of remaining upright? In order to gain insight to this, we calculated the mean values of the weights stored by the actor and critic at the end of learning for each simulation run. These weights are depicted in Figures 5.10, 5.11 and 5.12 for 9 months, 2years and 10 years, respectively.

Perhaps the easiest way to become oriented to these graphics is to start by examining the range of values depicted. At the side of each figure is a bar that represents the correspondence between the shading on the graph and the magnitude of the weight values depicted. Of specific interest here is a quick comparison of the scale observed in the actor weights (top panel) for each of the different ages. There was a clear progression across age such that the large values observed for the simulated 9 month-old (on the order of 10^{14}) were dramatically reduced for the 10 year old (on the order of 10^{1}). Of course, there is likely to be an influence of number of learning trials because, looking back at Equations 5.12 and 5.13, we note that while the learning rule for the critic weights utilized an eligibility trace that included a time-based decay on weight updates, there was no such decay for the actor. In other words, it seems that the structure of the model utilized in this study imposed no intrinsic limits on the magnitude to which the actor weights could climb, as they could be updated with every time-step and yet, were never decremented as were the critic weights. Whether this structure poses any practical problems across long-term learning remains an open question for further study.

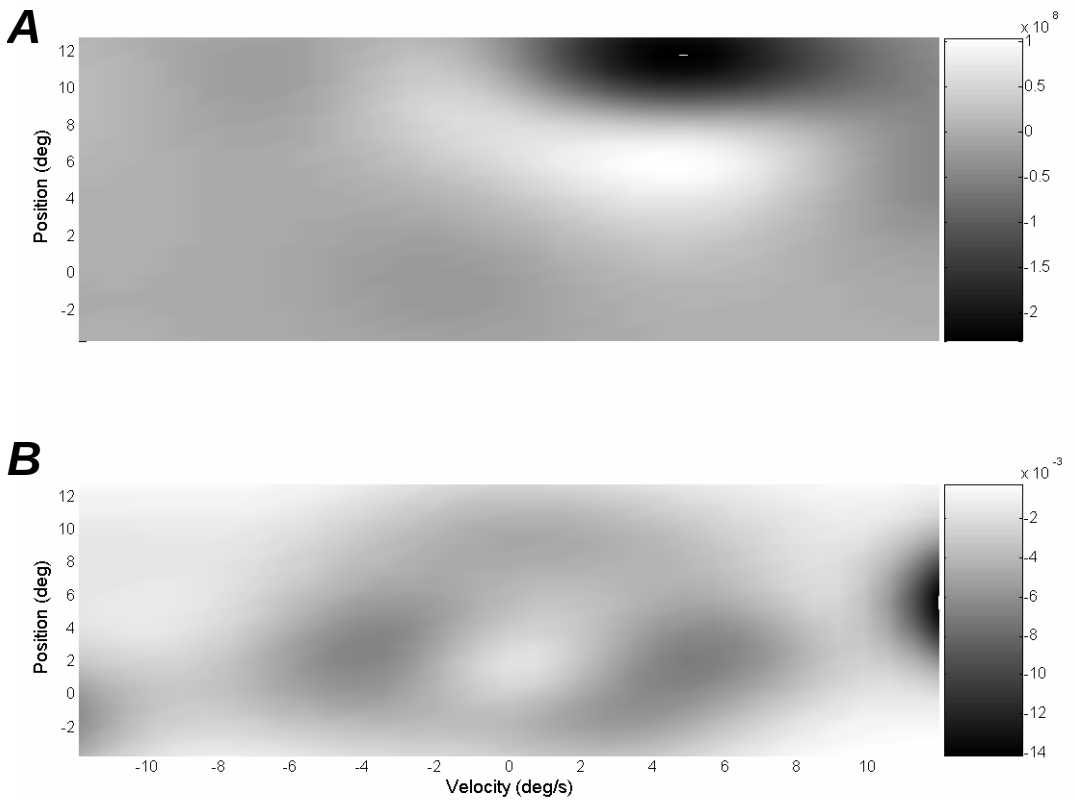


Figure 5.11. Final weights determined at the end of learning for a simulated 2 year old, by the (A) actor and (B) critic. Velocity is shown on the horizontal and position on the vertical axes; darker shading indicates increasingly negative weight values.

In addition to the larger magnitude of the weights, it is instructive to examine the relative positioning of the dark/light shading border within each represented state space. For example, it seems that regardless of simulated age, the weights learned within the critic reflect the intrinsic dynamics of the postural task. Keep in mind that any location with a higher value (lighter shading) is considered a state that the system has learned will lead to greater cumulative future reward, that is, a state that is likely to lead to remaining standing for a longer period of time. With this notion, it seems that all of the critics shown in Figures 5.10 – 5.12 have determined that the central state ($\theta = \dot{\theta} = 0$) is associated with high values (lighter shading). At the same time, the same can not be said for the actor. That is, there seem to be clear and interesting differences in the established

actor weights across simulated age. The actor weights depicted in the top panel of Figure 5.12 (10 year old), for instance, show a clear and expected relationship between the sign of the weights and the movement state of the system. That is, in this figure, we see that the system has learned to apply a positive control action (lighter shading) when the pendulum is in a negative position and moving with a negative velocity and, likewise, to apply a negative control action for any positive position/positive velocity combination.

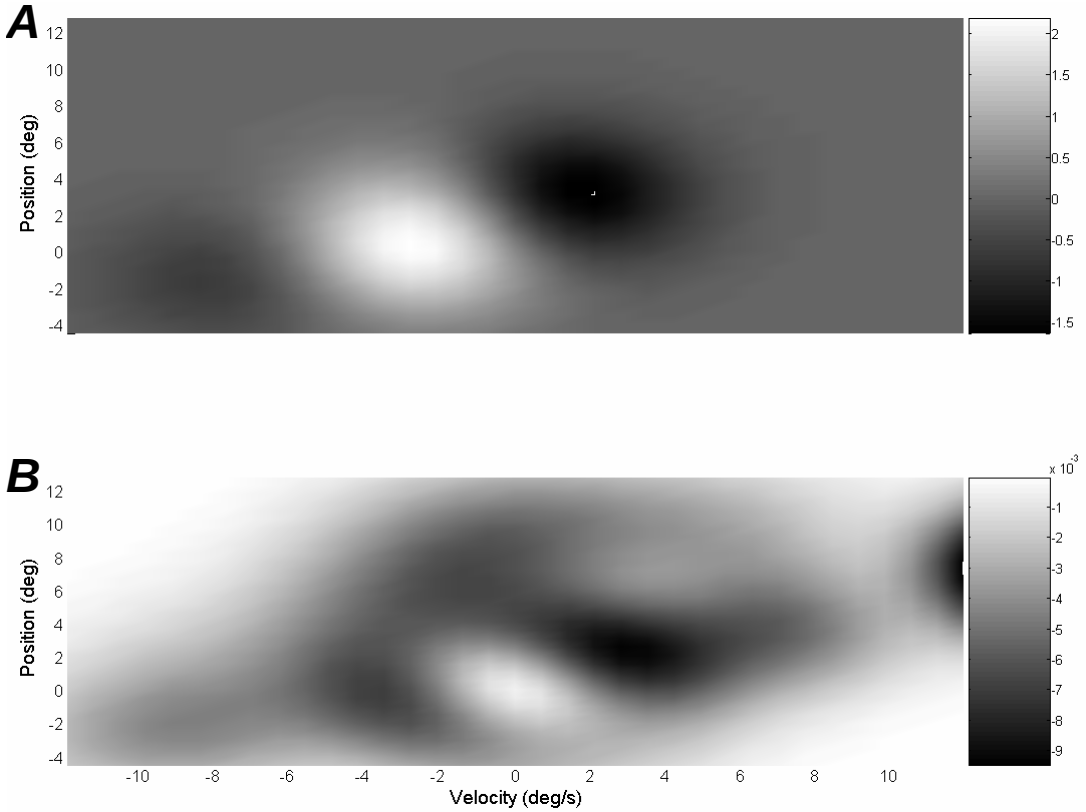


Figure 5.12. Final weights determined at the end of learning for a simulated 10 year old, by the (A) actor and (B) critic. Velocity is shown on the horizontal and position on the vertical axes; darker shading indicates increasingly negative weight values.

With this in mind, when we look at the learned control weights for the earlier two simulated ages (top panels of Figures 5.10 and 5.11), it seems that the *relationship* between positive and negative commands is preserved across age (the positive command is always to the left and/or lower than the negative command), but that this

positive/negative border appears displaced within the behavioral state space. Of particular interest is how it seems that this border 'moves' more dramatically along the velocity (horizontal axis) with increased simulated age than it does along the position (vertical axis). This observation appears consistent with the conclusion that postural development involves active modulation of sway velocity, but, of course, seems an ideal starting point for future study using this methodology.

Discussion

Overall, the simulation data presented in this study provided important information for facilitating interpretations of developmental changes in human postural sway. First, it was clearly shown that a system depicted as increasingly stochastic through inclusion of noise at various physiologically-relevant locations within the model produced behavior consistent with that which has been observed in humans. Moreover, while models that lack such sources of noise also produced similar overall results in terms of being able to learn what a human learns, there were important, nontrivial differences that should be considered in future modeling endeavors with this type of framework. Of more impact is that the application of the most 'physiologically accurate' model enabled assessment and replication of effects that have been observed across human postural development. That is, strong effects for changes in rate properties of sway with increased age and physical growth. Together the results of the two experiments presented in this study are encouraging for future applications and more detailed analyses aimed at understanding and carefully disentangling the various sources of change in human postural development.

Overall, two important results were found in this study. First, it is clear that, prior to the direct application of even the most compelling models extant in the literature, it is worthwhile to examine the correspondence between the output of that model and the associated human behavior. In the first of two experiments in this study, we examined the postural sway learnt by a model consistent with 'cutting-edge' modeling efforts from the engineering literature (Doya, 2000). Indeed, the continuous-time, continuous-space formulation that was developed by Doya has afforded applications to highly complex systems such as a real, autonomous multi-link robot that was able to learn to stand from an intial starting position of laying on the ground (Morimoto & Doya, 2001) as well as the 'simpler' multilink inverted pendulum and the cart-pole swing-up balancing testbeds (Doya, 1997; Si & Wang, 2001). It, of course, should go without saying that this model was of considerable advantage to the current investigation as well. At the same time, our analysis revealed that while this advanced and efficient model enabled robust success at achieving the goal (learning to stand), it did not ultimately provide data reflective of the type that motivate our questions. That is, while Doya and others have shown that powerful learning architectures may be formulated to achieve success at highly complex motor tasks, such architectures are not necessarily structured in a manner consistent with the human sensorimotor system. More to the point, comparison of human data with such models is perhaps most instructive when we begin to look for how the human system differs from such efficient and well-engineered learning systems. Perhaps the real lessons reside in not only the different assumptions that go into such models (i.e. where to put the noise), but also in the *differing goals* of a system engineered for maximal efficiency as compared with natural, biological systems that are not so much engineered as they are

adapted for broad functionality in a complex world. While the robotic system has only to learn to stand, the human must concurrently learn neuromuscular 'tunings' and associations to support many skillful and complex behaviors including standing, walking, reaching and so on.

A second broad lesson to be learned from the current study is that thoughtful application of extant models can and ultimately will lead to insights into human behavior that may never be readily available in analysis of empirical observations. That is, while on the surface the results of this study largely replicated and validated what should be expected in terms of the relationship between learning and growth in postural development, it also opened important doors to future areas of focus. Indeed, it would be unrealistic to expect that, somehow, the basic physical realities of human growth could eventually be separated from development in order to make way for the more 'theoretically-grounded mechanisms'. Rather, as originally discussed by Thelen (1986), growth is one subcomponent of a complex system of many subcomponents, each with its own ontogenetic course. Thus, it is doubtless that, as shown in this study, the influence of changing physical morphology is an important part of the overall explanation of human postural development. Yet, to consider such monistic conclusions as the ultimate explanation of postural development would be both naïve and myopic. In an ideal world, where the road leads from analyses such as those employed in the current study is towards the development of theoretically-motivated explanations that include an understanding of how the human develops complex, adaptive behaviors that are appropriate for, rather than in spite of, their changing body.

In terms of the detailed analyses, there seem to be some clear directions implicated by the results of the current study. Of particular interest from Experiment 1 was the noise × stiffness interaction observed for the rate-related properties of postural sway. Recall that in the absence of noise, the postural behavior that was learned by the system was of particularly low magnitude, low velocity and high frequency excursions. In such a scenario, it seems that the behavior that was learned gave the appearance of being highly refined and, as such, had little need for redundant stabilizing mechanisms such as a passive spring-like component. That is, with or without the influence of a such a passive component, relatively deterministic behavior ended up being highly stable. But, of course, caution is warranted in drawing such a conclusion based only on observations of low variability. It may be the case that, rather than being highly stable, such a system would be quite unstable in the face of unexpected perturbations whereas a noisier system that operates on a larger scale of motion, but also includes passive stabilizing factors, would be more robust to potentially harmful perturbations. Clearly it would be possible, and we would argue warranted, to use this same modeling approach to test this prediction. By continuing the delineate the sources of stability on human behavior in general, and in human postural behavior in specific, it is possible to advance the understanding of both rehabilitative training and developmental intervention.

In addition to utilizing computational approaches to advance the understanding of human behavior, this study also contributes an important caveat to the modeling community. That is, while increasingly sophisticated efforts continue to emerge in the use of artificial and computational systems to emulate human behavior, it is important to resist the temptation to optimistically generalize positive findings as truthful

representations of the actual structure of human behavior. Take, for example, our qualitative discussion of the actor and critic weights resulting from learning. Here, it was tempting to argue that the observation of very large weights that decreased with age validated the computational structure of the model. That is, this observation of inordinately large weight values appeared, on the surface, to be consistent with what we know about 'poor calibration' of human infant postural responses during early development (Bertenthal et al., 1997; Lee & Aronson, 1974; Metcalfe et al., 2005b; Sveistrup & Woollacott, 1996; Woollacott et al., 1987). However, more careful consideration of this result indicated a simpler and much less enlightening answer; it seems that the updating rule for the actor may also need an eligibility trace as in the original formulation of the reinforcement learning algorithm (Barto et al., 1983; Sutton & Barto, 1998). By lacking a mechanism for decrementing, as well as incrementing what is learned, the weights in the system will grow without bound over an infinite number of trials. Likewise, although the results of Experiment 2 provided compelling information regarding the relationship between physical maturation and learning, more details are needed to understand the intricacies of this interaction. For instance, this study did not systematically manipulate the structure of the state-space as it related to learning and growth but rather, a plausible, but general representation of the state-space and its associated reward function were imposed on the system to facilitate other goals of this study. However, without systematically examining how the human system establishes these variables, such as has been investigated through adaptive GRBF networks for non-biological systems (Morimoto & Doya, 2001; Singla et al., 2007), our conclusions will remain more speculative than informative.

The reason for concluding with these seemingly detailed examples regarding areas left open by our effort is thus: we must be cautious in our interpretations of our models. Without a healthy level of skepticism, what is a computational artifact could, in the hands of a skillful writer, become a part of the dogma regarding a given human behavior and this type of misrepresentation could ultimately mislead future research. By the same token, assessment of the assumptions and close scrutiny of the details within a given model reveal a variety of avenues available for future empirical and theoretical examinations. In this study, we have provided important formal insights into the relationship between physical maturation and sensorimotor learning of postural control. That is, we have seen that the system is best captured as (a) having intrinsic stochasticity within all major subcomponents including sensory, motor and decision processes, (b) this stochasticity may facilitate, as opposed to inhibit, learning of complex sensorimotor behaviors and (c) that the rate and nature of learning is directly impacted by the changing physical structure of the body. Beyond our results, however, we have given clear rationale to formalized future investigations of the relationship between physical growth and sensorimotor tuning in terms of how the physical body impacts the mapping of the behavioral state-space in terms of both estimation (e.g. value function) and control (e.g. action policy) parameters. Further, these data have indicated that investigations that ignore the influence of changing physical dynamics will only render an incomplete understanding of human postural development.

Chapter 6

Overall conclusions

The science and study of human behavior and its development is advancing at a tremendous pace in the modern era. Innovations in technology, advancements in computational methods and increased multidisciplinary, collaborative efforts are all contributing to a new and exciting era in the understanding of humanity. The studies contained in this dissertation represent such a confluence of factors. That is, standing on the foundations of the theories and concepts advanced by behavioral, biological and computational scientists working in advance of our research, we have provided important insights towards the understanding of a specific, but fundamental human behavior: the development of upright standing.

In the first two studies (Chapters 2 and 3), new insights were generated regarding detailed kinematic changes in postural sway during the acquisition and subsequent refinement of upright stance and locomotion. In short, we observed that changes in human stability encompass a process of continued refinement of rate-related, rather than amplitude-related, properties of sway. In Chapter 2, we exploited the method of stabilogram-diffusion analysis (Collins & De Luca, 1993) to facilitate testing and assessment of the unperturbed postural sway of infants and, through this study, were able to show that while infants seem to preserve a certain magnitude of sway during the first year of independent walking, they appear to actively modulate the rate-related properties of sway excursions. Moreover, this finding was counter to what would have been expected based on comparisons of infants with older children and adults (Newell et al.,

1997; Riach & Hayes, 1987); that is, that the development of postural sway embodied a reduction, rather than preservation of the magnitude of sway variability.

Building on our new insights into the intrinsic variability of infant posture, we devised the analyses presented in Chapter 3 to expand our understanding of development of sensorimotor integration (e.g. the phenomenon of 'coupling') in postural tasks (Barela et al., 1999; Barela et al., 2000; Bertenthal et al., 1997; Bertenthal et al., 2000; Bertenthal & Bai, 1989; Delorme et al., 1989; Lee & Aronson, 1974). In this study, we assessed longitudinal data regarding the temporal and spatial coordination between infant's postural sway and the motion of a sensory-mechanical stimulus (light hand contact with a gently oscillating surface). We began with the assumption that it is essential to assess moment-by-moment variability in the organization of infant's postural responses to oscillatory stimuli in order to gain a complete understanding of the development of those same responses. In particular, we chose to assess the infant responses with an uncommon application of analysis techniques from the electroencephalographic (EEG) literature rather than by utilizing standard linear systems techniques that are confounded in the presence of within-trial variability due to non-stationary behavior. By choosing an event-related methodology (McDowell et al., 2002; Pfurtscheller, 1996) aimed at quantifying, as opposed to reducing and eliminating, the intrinsic cycle-by-cycle variability in sway responses to a dynamic stimulus, we revealed that longitudinal development of the 'coupling phenomenon' involves modulation of the rate-related aspects of stance corrections. In this case, it was the *temporal stability* of the within-trial postural response to oscillating stimuli that changed most robustly with increased postural experience.

In the final analysis, we adopted a new method to facilitate testing of the inferences and conclusions from our previous works. Based on our empirical observations of the associations between changes in posture and upright walking experience, we had come to an understanding of postural development as a process facilitated by exploratory, or experienced-based, sensorimotor learning. As a result, in Chapter 5, we presented a simulation study that implemented a computational method aimed at formalizing the assessment of the inferences we made in our previous empirical works. In conceiving this study, we looked to the machine-learning literature for an encompassing framework that would afford a detailed characterization of exploratory sensorimotor learning while including physical constraints, such as growth, on the developing system. In the subsequent application of an unsupervised, reinforcement learning model (Barto et al., 1983; Berthier et al., 2005; Morimoto & Doya, 2001; Sutton & Barto, 1998), we were able to provide clear examples of how experienced-based learning interacts with intrinsic maturational factors such as growth. To this end, we not only replicated the main results of our previous longitudinal studies regarding fundamental changes in rate-related properties of postural sway, but we did so through a combination of physical growth, changes in 'effective stiffness' and active, experience-based sensorimotor learning. In short, we provided evidence leading to the validation of our earlier interpretations of potential sources of behavioral change during postural development while revealing important directions for future formalized, or model-based, investigations.

As this work has been largely targeted at answering *basic* questions regarding human postural development, we believe that the next step should be one of building. In

other words, using concepts and observations from the research presented in this dissertation in combination with the extant data within the developmental literature, increasingly refined and comprehensive models of human postural development can be formulated and assessed against the barometer of actual human data. Indeed, the observations from all of our empirical data (Chen et al., 2007a; Chen et al., 2007b; Metcalfe et al., 2005b; Metcalfe et al., 2005a) will continue to provide a basis for future assessment, replication and validation. Moreover, the merging of the data we have provided with extant data regarding other aspects of postural development, such as muscular response patterns (Hadders-Algra et al, 1996; Sveistrup et al, 1996; Woollacott et al, 1987) and sensorimotor coupling (Bertenthal et al., 1997; Bertenthal et al., 2000; Jouen et al., 2000), through models will enable deeper insights to the essential nature of human postural control.

We view both increased multidisciplinary efforts and the application of formalized models as essential to interpreting empirical observations of behavioral change with development. We are hopeful that future efforts eventually begin to focus on broader inter-relationships amongst fundamental skills, for example understanding observations indicating an influence of posture on the course of reaching development (Corbetta & Bojczyk, 2002; Rochat, 1992) as well as the vast influence of self-produced locomotion on a myriad of cognitive, perceptual and motor skills (Campos et al., 2000). Indeed, the lessons learned from efforts such as that embodied in the current dissertation, should guide the formulation and continued refinement of models with greater capacity for testing the interesting questions regarding sources of change in human sensorimotor development.

Appendices

Appendix A: Informed consent – Parental permission form I

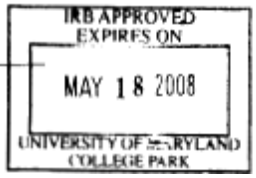
Parental Permission (A)

Project	Postural development and perception-action coupling.
Statement of Subject's Age	This is a research project being conducted by Dr. Jane E. Clark at the University of Maryland, College Park. We are inviting you to participate in this research project because you are over 18 years of age and are the parent or legal guardian of 0- to 3-year olds.
Purpose	This study is to examine how infants at different developmental periods use surface contact and vision while sitting and standing upright.
Procedure	The procedure involves monthly visits to the Motor Behavior Lab of 40-60 minutes each for the first 4-5 months and bimonthly visits for the next 10-15 months. The visits will take place over a period of about one and half year as your child progresses from sitting to nine months of walking experience. Bimonthly visits will begin once your child begins standing and will be scheduled within five days of each other. Your child will sit in a modified infant seat or stand on a small pedestal in touch or/and visual condition. In the touch condition, your child will sit/stand independently or with touching a slightly moving contact surface with the right hand. In the vision condition, your child will be presented with visual displays of gently moving random dots projected on the front and side walls. The touch surface, the seat and the standing pedestal contain instruments that measure the force the child applies to them. Small, light-weight markers will be placed on the infant's head, upper back, and lower back to measure the infant's body movements. There will be 17-22 trials per testing session depending on the infant. Each trial will be 60-90 seconds and the testing session will be videotaped. After completing each postural testing session, you will receive $15.00 dollars. In addition to postural test, your child will also be assessed by the Bayley Scale of Infant Development at 6, 9, 12, 18 months of age. The developmental test includes mental and motor assessment and takes about 30-45 minutes.
Risks	During the experiment, the infant may lose control of his/her balance. Prompt assistance will be provided by either the parent and/or experimenter who will be standing next to your child. There are no other known risks and no long-term effects associated with this study.
Confidentiality	All information collected in this study is confidential and your child's name will not be identified at any time during reports and presentations. All information will be coded and stored in a locked cabinet. Your information may be shared with representatives of the University of Maryland, College Park or governmental authorities if you or someone else is in danger or if we are required to do so by law.
Benefits; Freedom to Withdraw and Ask Questions	You and your child's participation is completely voluntary. This experiment is not designed to clinically test or treat your child or to help the child personally. This investigation seeks l to earn more about the postural control of infants. You are free to ask questions or to withdraw your child from participation at any time without penalty. You could have a signed copy of this consent form and the investigators will provide you with the results from this study.
Principal Investigator	Jane E. Clark, Ph.D. 2351 Health and Human Performance Building University of Maryland College Park, MD 20742-2611 Lab Phone: (301) 405-2574 Office Phone: (301) 405-2450

If you have questions about your rights as a research subject or wish to report a research-related injury, please contact: Institutional Review Board Office, University of Maryland, College Park, Maryland, 20742; (e-mail) irb@deans.umd.edu; (telephone) 301-405-0678

Name of Infant _____ Birthday _____

Signature of Responsible Party _____ Date _____



Appendix B: Informed consent – Parental permission form II

Parental Permission Form (C)
For Video and Image Illustration Purposes

Project — Postural development and perception-action coupling.

Purpose of this form — Often, in disseminating information from our research, it is useful to include images and/or video clips from testing sessions with the infants. Examples of such cases include: (1) poster and podium presentations at scholarly meetings and conferences, (2) instructional purposes, and (3) on our internet site. The use of such images assists in a number of ways, particularly for validating our protocols and demonstrating the safety of our testing environment.

In this form, we seek your permission to use images recorded with your infant for these purposes. Below, you will see a number of options. Please place your initials next to the uses that you are willing to allow.

Confidentiality — All images and videos recorded in this study are confidential and that your child's name will not be identified at any time for reports and presentations. All images and videos will be coded in a manner that protects your child's identity and stored in a locked cabinet.

Statement of consent — Videos and images are recorded with your child for the confidential records of the Motor Development Research Team in the Cognitive Motor Behavior Laboratory. Below are your intentions regarding their use:

_____ I am willing to allow use of the images for inclusion in presentations at scholarly meetings and conferences.

_____ I am willing to allow use of the images for inclusion in scientific publication

_____ I am willing to allow use of the images for instructional purposes, including courses taught in the Department of Kinesiology at the University of Maryland.

_____ I am willing to allow use of the images for inclusion in the motor development website at the University of Maryland.

_____ I do not want the images used for anything other than internal laboratory purposes.

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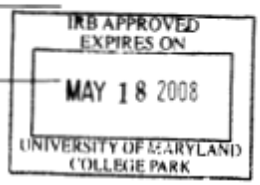
If you have questions about your rights as a research subject or wish to report a research-related injury, please contact: Institutional Review Board Office, University of Maryland, College Park, Maryland, 20742; (e-mail) irb@deans.umd.edu; (telephone) 301-405-0678

_____ Name of Infant

_____ Birthday

_____ Signature of Responsible Party

_____ Date



References

Adolph, K. E. (1997). Learning in the development of infant locomotion. *Monographs of the Society for Research in Child Development, 62,* 1-158.

Adolph, K. E. (2000). Specificity of learning: Why infants fall over a veritable cliff. *Psychological Science, 11,* 290-295.

Adolph, K. E. (2002). Learning to keep balance. In R.Kail (Ed.), *Advances in child development and behavior* (pp. 1-40). Amsterdam: Elsevier Science.

Adolph, K. E., Eppler, M. A., & Gibson, E. J. (1993). Crawling versus walking infants' perception of affordances for locomotion over sloping surfaces. *Child Development, 64,* 1158-1174.

Adolph, K. E., Vereijken, B., & Denny, M. A. (1998). Learning to crawl. *Child Development, 69,* 1299-1312.

Alexandrov, A. V., Frolov, A. A., Horak, F. B., Carlson-Kuhta, P., & Park, S. (2005). Feedback equilibrium control during human standing. *Biological Cybernetics, 93,* 309-322.

Anderson, D. I., Campos, J. J., Anderson, D. E., Thomas, T. D., Witherington, D. C., Uchiyama, I. et al. (2001). The flip side of perception-action coupling: Locomotor experience and the ontogeny of visual-postural coupling. *Human Movement Science, 20,* 461-487.

Barela, J. A., Godoi, D., Freitas, P. B., & Polastri, P. F. (2000). Visual information and body sway coupling in infants during sitting acquisition. *Infant Behavior and Development, 23,* 285-297.

Barela, J. A., Jeka, J. J., & Clark, J. E. (1999). The use of somatosensory information during the acquisition of independent upright stance. *Infant Behavior and Development, 22,* 87-102.

Barto, A. G., Sutton, R. S., & Anderson, C. W. (1983). Neuronlike adaptive elements that can solve difficult learning problems. *IEEE Transactions on Systems, Man and Cybernetics, 13,* 834-846.

Bayley, N. (1993). *Bayley scales of infant development*. (2 ed.) San Antonio, TX: The Psychological Corporation.

Bertenthal, B. I. (1996). Origins and early development of perception, action, and representation. *Annual Review of Psychology, 47,* 431-459.

Bertenthal, B. I. & Bai, D. L. (1989). Infants Sensitivity to Optical-Flow for Controlling Posture. *Developmental Psychology, 25,* 936-945.

Bertenthal, B. I., Boker, S. M., & Xu, M. (2000). Analysis of the perception-action cycle for visually induced postural sway in 9-month-old sitting infants. *Infant Behavior and Development, 23,* 299-315.

Bertenthal, B. I., Campos, J. J., & Kermoian, R. (1994). An epigenetic perspective on the development of self-produced locomotion and its consequences. *Current Directions in Psychological Science, 3,* 140-145.

Bertenthal, B. I. & Clifton, R. K. (1998). Perception and action. In D.Kuhn & R. S. Seigler (Eds.), *Handbook of child psychology, Vol. 2: Cognition, perception, and language* (5 ed., pp. 51-102). New York: John Wiley.

Bertenthal, B. I., Rose, J. L., & Bai, D. L. (1997). Perception - action coupling in the development of visual control of posture. *Journal of Experimental Psychology.Human Perception and Performance., 23,* 1631-1643.

Berthier, N. E. (1996). Learning to reach: A mathematical model. *Developmental Psychology, 32,* 811-823.

Berthier, N. E., Rosenstein, M. T., & Barto, A. G. (2005). Approximate optimal control as a model for motor learning. *Psychological Review, 112,* 329-346.

Berthoz, A. & Viaud-Delmon, I. (1999). Multisensory integration in spatial orientation. *Current Opinion in Neurobiology, 9,* 708-712.

Borghese, N. A. & Calvi, A. (2003). Learning to maintain upright posture: What can be learned using adaptive neural network models? *Adaptive Behavior, 11,* 19-35.

Brenière, Y. & Bril, B. (1998). Development of postural control of gravity forces in children during the first 5 years of walking. *Experimental Brain Research, 121,* 255-262.

Bruner, J. S. (1973). Organization of early skilled action. *Child Development, 44,* 1-11.

Buchanan, J. J. & Horak, F. B. (1999). Emergence of postural patterns as a function of vision and translation frequency. *Journal of Neurophysiology, 81,* 2325-2339.

Bugmann, G. (1998). Normalized Gaussian radial basis function networks. *Neurocomputing, 20,* 97-110.

Butterworth, G. & Hicks, L. (1977). Visual proprioception and postural stability in infancy. A developmental study. *Perception, 6,* 255-262.

Cairns, R. B. (1998). The making of developmental psychology. In R.M.Lerner (Ed.), *Handbook of child psychology* (pp. 189-220). New York: MacMillan.

Campos, J. J., Anderson, D. I., Barbu-Roth, M. A., Hubbard, E. M., Hertenstein, M. J., & Witherington, D. C. (2000). Travel broadens the mind. *Infancy, 1,* 149-219.

Charlesworth, W. R. (1986). Darwin and Developmental Psychology - 100 years later. *Human Development, 29,* 1-4.

Chen, L.-C., Metcalfe, J. S., Chang, T.-Y., Jeka, J. J., & Clark, J. E. (2007a). The development of infant upright posture: Sway less or sway differently? *Experimental Brain Research, In Press*.

Chen, L.-C., Metcalfe, J. S., Jeka, J. J., & Clark, J. E. (2007b). Two steps forward and one back: Learning to walk affects infants sitting posture. *Infant Behavior and Development, 30,* 16-25.

Chester, V. L. & Jensen, R. K. (2005). Changes in infant segment inertias during the first three months of independent walking. *Dynamic Medicine, 4,* 9.

Chiari, L., Cappello, A., Lenzi, D., & Della, C. U. (2000). An improved technique for the extraction of stochastic parameters from stabilograms. *Gait & Posture, 12,* 225-234.

Chow, C. C., Lauk, M., & Collins, J. J. (1999). The dynamics of quasi-static posture control. *Human Movement Science, 18,* 725-740.

Clark, J. E. (1995). On becoming skillful: Patterns and constraints. *Research Quarterly for Exercise and Sport, 66,* 173-183.

Clark, J. E. (1997). A dynamical systems perspective on the development of complex adaptive skill. In C.Dent-Read & P. Goldring-Zukow (Eds.), *Evolving*

explanations of development (pp. 383-406). Washington, DC: American Psychological Association.

Clark, J. E. & Metcalfe, J. S. (2002). The mountain of motor development: A metaphor. In J.E.Clark & J. Humphrey (Eds.), *Motor development: Research and reviews* (pp. 163-190). Reston, VA.: NASPE Publications.

Clark, J. E. & Phillips, S. J. (1987). The step cycle organization of infant walkers. *Journal of Motor Behavior, 19,* 421-433.

Clark, J. E. & Phillips, S. J. (1993). A longitudinal study of intralimb coordination in the first year of independent walking: a dynamical systems analysis. *Child Development, 64,* 1143-1157.

Clark, J. E. & Whitall, J. (1989). What Is Motor Development - the Lessons of History. *Quest, 41,* 183-202.

Clark, J. E., Whitall, J., & Phillips, S. J. (1988). Human interlimb coordination: The first 6 months of independent walking. *Developmental Psychobiology, 21,* 445-456.

Clearfield, M. W. (2004). The role of crawling and walking experience in infant spatial memory. *Journal of Experimental Child Psychology, 89,* 214-241.

Collins, J. J. & De Luca, C. J. (1993). Open-loop and closed-loop control of posture: A random-walk analysis of center-of-pressure trajectories. *Experimental Brain Research, 95,* 308-318.

Collins, J. J. & De Luca, C. J. (1994). Random walking during quiet standing. *Physical Review Letters, 73,* 764-767.

Collins, J. J. & De Luca, C. J. (1995). Upright, correlated random walks: A statistical-biomechanics approach to the human postural control system. *Chaos, 5,* 57-63.

Corbetta, D. & Bojczyk, K. E. (2002). Infants return to two-handed reaching when they are learning to walk. *Journal of Motor Behavior, 34,* 83-95.

Delignières, D., Deschamps, T., Legros, A., & Caillou, N. (2003). A methodological note on nonlinear time series analysis: Is the open- and closed-loop model of Collins and De Luca (1993) a statistical artifact? *Journal of Motor Behavior, 35,* 86-96.

Delorme, A., Frigon, J., & Lagacé, C. (1989). Infants' reactions to visual movement of the environment. *Perception, 18,* 667-673.

Deluca, C. J. (1997). The use of surface electromyography in biomechanics. *Journal of Applied Biomechanics, 13,* 135-163.

Dijkstra, T. M. H. (2000). A gentle introduction to the dynamic set-point model of human postural control during perturbed stance. *Human Movement Science, 19,* 567-595.

Doya, K. (1997). Efficient nonlinear control with actor-tutor architecture. In M.C.Mozer, M. I. Jordan, & T. Petsche (Eds.), *Advances in neural information processing systems* (pp. 1012-1018). Cambridge, MA: The MIT Press.

Doya, K. (2000). Reinforcement learning in continuous time and space. *Neural Computation, 12,* 219-245.

Duarte, M. & Zatsiorsky, V. M. (1999). Patterns of center of pressure migration during prolonged unconstrained standing. *Motor Control, 3,* 12-27.

Enoka, R. M. (2002). *Neuromechanics of human movement*. (3 ed.) Champaign, IL: Human Kinetics.

Fitzpatrick, R., Burke, D., & Gandevia, S. C. (1996). Loop gain of reflexes controlling human standing measured with the use of postural and vestibular disturbances. *Journal of Neurophysiology, 76,* 3994-4008.

Forssberg, H. & Nashner, L. M. (1982). Ontogenetic development of postural control in man: Adaptation to altered support and visual conditions during stance. *The Journal of Neuroscience, 2,* 545-552.

Foster, E. C., Sveistrup, H., & Woollacott, M. H. (1996). Transitions in visual proprioception: A cross-sectional developmental study of the effect of visual flow on postural control. *Journal of Motor Behavior, 28,* 101-112.

Gagne, P. & Dayton, C. M. (2002). Best regression using information criteria. *Journal of Modern Statistical Methods, 1,* 479-488.

Gibson, E. J. (1987). Introductory essay: What does infant perception tell us about theories of perception? *Journal of Experimental Psychology.Human Perception and Performance., 13,* 515-523.

Gibson, E. J. & Schmuckler, M. A. (1989). Going somewhere: An ecological and experimental approach to development of mobility. *Ecological Psychology, 1,* 3-25.

Hadders-Algra, M., Brogren, E., & Forssberg, H. (1996). Ontogeny of postural adjustments during sitting in infancy: Variation, selection and modulation. *The Journal of Physiology, 493 (Pt 1),* 273-288.

Hadders-Algra, M., Brogren, E., & Forssberg, H. (1997). Nature and nurture in the development of postural control in human infants. *Acta Paediatrica Supplement, 422,* 48-53.

Hadders-Algra, M., Brogren, E., & Forssberg, H. (1998). Development of postural control--differences between ventral and dorsal muscles? *Neuroscience and Biobehavioral Reviews, 22,* 501-506.

Hammock, E. A. D. & Levitt, P. (2006). The discipline of neurobehavioral development: The emerging interface of processes that build circuits and skills. *Human Development, 49,* 294-309.

Hirschfeld, H. & Forssberg, H. (1992). Development of anticipatory postural adjustments during locomotion in children. *Journal of Neurophysiology, 68,* 542-550.

Hofsten, C. v. (1997). On the early development of predictive abilities. In C.Dent-Read & P. Zukow-Goldring (Eds.), *Evolving explanations of development: Ecological approaches to organism-environment systems* (pp. 163-194). Washington, D.C.: American Psychological Association.

Horak, F. B. & MacPhearson, J. M. (1996). Postural orientation and equilibrium. In L.B.Rowell & J. T. Shepherd (Eds.), *Handbook of physiology* (pp. 255-292). New York: Oxford University Press.

Horak, F. B., Nashner, L. M., & Diener, H. C. (1990). Postural strategies associated with somatosensory and vestibular loss. *Experimental Brain Research, 82,* 167-177.

Ishii, S., Yoshida, W., & Yoshimoto, J. (2002). Control of exploitation-exploration meta-parameter in reinforcement learning. *Neural Networks, 15,* 665-687.

Jacobs, R. (1997). Control model of human stance using fuzzy logic. *Biological Cybernetics, 77,* 63-70.

Jeka, J. J. & Lackner, J. R. (1994). Fingertip contact influences human postural control. *Experimental Brain Research, 100,* 495-502.

Jeka, J. J., Oie, K. S., & Kiemel, T. (2000). Multisensory information for human postural control: Integrating touch and vision. *Experimental Brain Research, 134,* 107-125.

Jeka, J. J., Oie, K. S., Schöner, G. S., Dijkstra, T. M. H., & Henson, E. (1998). Position and velocity coupling of postural sway to somatosensory drive. *Journal of Neurophysiology, 79,* 1661-1674.

Jensen, R. K., Sun, H., Treitz, T., & Parker, H. E. (1997). Gravity constraints in infant motor development. *Journal of Motor Behavior, 29,* 64-71.

Johansson, R. & Magnusson, M. (1989). Determination of characteristic parameters of human postural dynamics. *Acta Oto-laryngologica.Supplementum, 468,* 221-225.

Johansson, R., Magnusson, M., & Akesson, M. (1988). Identification of human postural dynamics. *IEEE Transactions on Bio-medical Engineering, 35,* 858-869.

Jordan, M. I. (1996). Computational aspects of motor control and learning. In H.Heuer & S. W. Keele (Eds.), *Handbook of Perception and Action, Vol. II: Motor Skills* (pp. 71-120). New York: Academic Press.

Jouen, F., Lepecq, J.-C., Gapenne, O., & Bertenthal, B. I. (2000). Optic flow sensitivity in neonates. *Infant Behavior and Development, 23,* 271-284.

Kiemel, T., Oie, K. S., & Jeka, J. J. (2002). Multisensory fusion and the stochastic structure of postural sway. *Biological Cybernetics, 87,* 262-277.

Kiemel, T., Oie, K. S., & Jeka, J. J. (2006). Slow dynamics of postural sway are in the feedback loop. *Journal of Neurophysiology, 95,* 1410-1418.

Kooij, H. v. d., Jacobs, R., Koopman, B., & Grootenboer, H. (1999). A multisensory integration model of human stance control. *Biological Cybernetics, 80,* 299-308.

Kuniyoshi, Y. & Sangawa, S. (2006). Early motor development from partially ordered neural-body dynamics: Experiments with a cortico-spinal-musculo-skeletal model. *Biological Cybernetics, 95,* 589-605.

Kuo, A. D. (1995). An optimal control model for analyzing human postural balance. *IEEE Transactions on Bio-medical Engineering, 42,* 87-101.

Kuo, A. D. (2002). The relative roles of feedforward and feedback in the control of rhythmic movements. *Motor Control, 6,* 129-145.

Ledebt, A. & Bril, B. (2000). Acquisition of upper body stability during walking in toddlers. *Developmental Psychobiology, 36,* 311-324.

Ledebt, A., Bril, B., & Brenière, Y. (1998). The build-up of anticipatory behaviour. An analysis of the development of gait initiation in children. *Experimental Brain Research, 120,* 9-17.

Lee, D. N. & Aronson, E. (1974). Visual proprioceptive control of standing in human infants. *Perception & Psychophysics, 15,* 529-532.

Lerner, R. M. (1998). Theories of human development: Contemporary perspectives. In R.M.Lerner (Ed.), *Handbook of child psychology: Volume 1. Theoretical models of human development* (5 ed., pp. 1-24). New York: John Wiley.

Lestienne, F. G. & Gurfinkel, V. S. (1988). Postural control in weightlessness: A dual process underlying adaptation to an unusual environment. *Trends in Neuroscience, 11,* 359-363.

Loram, I. D., Maganaris, C. N., & Lakie, M. (2005). Active, non-spring-like muscle movements in human postural sway: How might paradoxical changes in muscle length be produced? *Journal of Physiology, 564,* 281-293.

Malina, R. M., Bouchard, C., & Bar-Or, O. (2004). *Growth, maturation and physical activity*. (2 ed.) Champaign, IL: Human Kinetics.

Mareschal, D. (2000). Object knowledge in infancy: Current controversies and approaches. *Trends in Cognitive Sciences, 4,* 408-416.

Mareschal, D., Plunkett, K., & Harris, P. (1999). A computational and neuropsychological account of object-oriented behaviours in infancy. *Developmental Science, 2,* 306-317.

McCollum, G. & Leen, T. K. (1989). Form and exploration of mechanical stability limits in erect stance. *Journal of Motor Behavior, 21,* 225-244.

McDowell, K., Jeka, J. J., Schöner, G., & Hatfield, B. D. (2002). Behavioral and electrocortical evidence of an interaction between probability and task metrics in movement preparation. *Experimental Brain Research, 144,* 303-313.

McGraw, M. B. (1932). From reflex to muscular control in the assumption of an erect posture and ambulation in the human infant. *Child Development, 3,* 291-297.

Metcalfe, J. S., Chen, L.-C., Chang, T.-Y., McDowell, K., Jeka, J. J., & Clark, J. E. (2005a). The temporal organization of posture changes during the first year of independent walking. *Experimental Brain Research, 161,* 405-416.

Metcalfe, J. S. & Clark, J. E. (2000). Somatosensory information affords the exploration of posture in newly walking infants and toddlers. *Infant Behavior and Development, 23,* 391-405.

Metcalfe, J. S., McDowell, K., Chang, T.-Y., Chen, L.-C., Jeka, J. J., & Clark, J. E. (2005b). Development of somatosensory-motor integration: An event-related analysis of infant posture in the first year of independent walking. *Developmental Psychobiology, 46,* 19-35.

Metta, G., Sandini, G., & Konczak, J. (1999). A developmental approach to visually-guided reaching in artificial systems. *Neural Networks, 12,* 1413-1427.

Morasso, P. G., Baratto, L., Capra, R., & Spada, G. (1999). Internal models in the control of posture. *Neural Networks, 12,* 1173-1180.

Morasso, P. G. & Sanguineti, V. (2002). Ankle muscle stiffness alone cannot stabilize balance during quiet standing. *Journal of Neurophysiology, 88,* 2157-2162.

Morasso, P. G. & Schieppati, M. (1999). Can muscle stiffness alone stabilize upright standing? *Journal of Neurophysiology, 82,* 1622-1626.

Morimoto, J. & Doya, K. (2001). Acquisition of stand-up behavior by a real robot using hierarchical reinforcement learning. *Robotics and Autonomous Systems, 36,* 37-51.

Morton, J. B. & Munakata, Y. (2005). Active versus latent representations: A neural network model of perseveration, dissociation and decalage. *Developmental Psychobiology, 40,* 255-265.

Nashner, L. M. (1976). Adapting reflexes controlling the human posture. *Experimental Brain Research, 26,* 59-72.

Nashner, L. M. & Peters, J. F. (1990). Dynamic posturography in the diagnosis and management of dizziness and balance disorders. *Neurologic Clinics, 8,* 331-349.

Nesselroade, J. R. & Schmidt McCollam, K. M. (2000). Putting the process in developmental processes. *International Journal of Behavioral Development, 24,* 295-300.

Newell, K. M. (1998). Degrees of freedom and the development of postural center of pressure profiles. In K.M.Newell & P. C. M. Molenaar (Eds.), *Applications of nonlinear dynamics to developmental process modeling* (pp. 63-84). Mahwah, N.J.: Lawrence Erlbaum.

Newell, K. M. & Molenaar, P. C. M. (1998). Introduction: Modeling development as dynamical systems. In K.M.Newell & P. C. M. Molenaar (Eds.), *Applications of nonlinear dynamics to developmental process modeling* (pp. 1-11). Mahwah, NJ: Lawrence Erlbaum.

Newell, K. M., Slobounov, S. M., Slobounova, E. S., & Molenaar, P. C. (1997). Stochastic processes in postural center-of-pressure profiles. *Experimental Brain Research, 113,* 158-164.

Oie, K. S., Kiemel, T., & Jeka, J. J. (2002). Multisensory fusion: Simultaneous re-weighting of vision and touch for the control of human posture. *Cognitive Brain Research, 14,* 164-176.

Overton, W. F. (1998). Developmental psychology: Philosophy, concepts, and methodology. In R.M.Lerner (Ed.), *Handbook of child psychology, Volume.1: Theoretical models of human development* (5 ed., pp. 107-188). New York: MacMillan.

Palmer, C. E. (1944). Studies of the center of gravity in the human body. *Child Development, 15,* 99-180.

Parisi, D. & Schlesinger, M. (2002). Artificial life and Piaget. *Cognitive Development, 17,* 1301-1321.

Peterka, R. J. (2000). Postural control model interpretation of stabilogram diffusion analysis. *Biological Cybernetics, 82,* 335-343.

Pfurtscheller, G. (1996). Event-related synchronization (ERS) in the alpha band - an electrophysiological correlate of cortical idling: A review. *International Journal of Psychophysiology, 24,* 39-46.

Prieto, T. E., Myklebust, J. B., Hoffmann, R. G., Lovett, E. G., & Myklebust, B. M. (1996). Measures of postural steadiness: Differences between healthy young and elderly adults. *IEEE Transactions on Bio-medical Engineering, 43,* 956-966.

Reed, E. S. (1989). Changing theories of postural development. In M.H.Woollacott & A. Shumway-Cook (Eds.), *Development of posture and gait across the lifespan* (pp. 3-24). Columbia, SC.: University of South Carolina Press.

Ressler, S. (1977). Anthrokids - Anthropometric Data of Children. http://www.itl.nist.gov/iaui/ovrt/projects/anthrokids/ [On-line].

Riach, C. L. & Hayes, K. C. (1987). Maturation of postural sway in young children. *Developmental Medicine and Child Neurology, 29,* 650-658.

Riley, M. A., Balasubramaniam, R., Mitra, S., & Turvey, M. T. (1998). Visual influences on center of pressure dynamics in upright posture. *Ecological Psychology, 10,* 65-91.

Riley, M. A., Wong, S., Mitra, S., & Turvey, M. T. (1997). Common effects of touch and vision on postural parameters. *Experimental Brain Research, 117,* 165-170.

Rochat, P. (1992). Self-sitting and reaching in 5- to 8- month old infants: The impact of posture and its development on early eye-hand coordination. *Journal of Motor Behavior, 24,* 210-220.

Roncesvalles, M. N., Woollacott, M. H., Brown, N., & Jensen, J. L. (2004). An emerging postural response: Is control of the hip possible in the newly walking child? *Journal of Motor Behavior, 36,* 147-159.

Sale, D. G. (1987). Influence of exercise and training on motor unit activation. In K.B.Pandolf (Ed.), *Exercise and sport science reviews.* (pp. 95-151). New York: MacMillan Publishing Co.

Schmuckler, M. A. & Gibson, E. J. (1989). The effect of imposed optical flow on guided locomotion in young walkers. *British Journal of Developmental Psychology, 7,* 193-206.

Schwarz, G. (1978). Estimating the dimension of a model. *Annals of Statistics, 6,* 461-464.

Shirley, M. N. (1931). *The first two years, a study of twenty-five babies: I. Postural and locomotor development*. Minneapolis, MN: University of Minnesota Press.

Shultz, T. R. (2003). *Computational developmental psychology*. Cambridge, MA: The MIT Press.

Si, J. & Wang, Y.-T. (2001). Online learning control by association and reinforcement. *IEEE Transactions on Neural Networks, 12,* 264-276.

Singla, P., Subbarao, K., & Junkins, J. L. (2007). Direction-dependent learning approach to radial basis function networks. *IEEE Transactions on Neural Networks, 18,* 203-222.

Stoffregen, T. A., Schmuckler, M. A., & Gibson, E. J. (1987). Use of central and peripheral optical flow in stance and locomotion in young walkers. *Perception, 16,* 113-119.

Sutton, R. S. & Barto, A. G. (1998). *Reinforcement learning: An Introduction*. Cambridge, MA: The MIT Press.

Sveistrup, H. & Woollacott, M. H. (1996). Longitudinal development of the automatic postural response in infants. *Journal of Motor Behavior, 28,* 58-70.

Sveistrup, H. & Woollacott, M. H. (1997). Practice modifies the developing automatic postural response. *Experimental Brain Research, 114,* 33-43.

Thelen, E. (1986). Development of coordinated movement: Implications for human development. In M.G.Wade & H. T. A. Whiting (Eds.), *Motor development in children: Aspects of coordination and control* (pp. 106-119). Boston, MA: Martin Nijhoff.

Thelen, E. (2000a). Grounded in the world: Developmental origins of the embodied mind. *Infancy, 1,* 3-28.

Thelen, E. (2000b). Motor development as foundation and future of developmental psychology. *International Journal of Behavioral Development, 24,* 385-397.

Thelen, E., Schöner, G., Scheier, C., & Smith, L. B. (2005). The dynamics of embodiment: A field theory of infant perseverative reaching. *Behavioral and Brain Sciences, 24,* 1-86.

Thelen, E. & Smith, L. B. (1994). *A dynamic systems approach to the development of cognition and action*. Cambridge, MA: The MIT Press.

Thelen, E. & Smith, L. B. (1998). Dynamic systems theories. In R.M.Lerner (Ed.), *Handbook of child psychology. Volume 1: Theoretical models of human development* (5 ed., pp. 563-634). New York: MacMillan.

Tresp, V., Hollatz, J., & Ahmad, S. (1997). Representing probabilistic rules with networks of Gaussian basis functions. *Machine Learning, 27,* 173-200.

Valsiner, J. (1998). The development of the concept of development: Historical and epistemological perspectives. In R.M.Lerner (Ed.), *Handbook of Child Psychology. Volume 1: Theoretical models of human development* (pp. 189-232). New York: MacMillan.

Wiener-Vacher, S. R., Toupet, F., & Narcy, P. (1996). Canal and otolith vestibulo-ocular reflexes to vertical and off vertical axis rotations in children learning to walk. *Acta Oto-Laryngologica, 116,* 657-665.

Winter, D. A., Patla, A. E., Prince, F., Ishac, M., & Gielo-Perczak, K. (1998). Stiffness control of balance in quiet standing. *Journal of Neurophysiology, 80,* 1211-1221.

Winter, D. A., Patla, A. E., Rietdyk, S., & Ishac, M. G. (2001). Ankle muscle stiffness in the control of balance during quiet standing. *Journal of Neurophysiology, 85,* 2630-2633.

Winter, D. A., Prince, F., Frank, J. S., Powell, C., & Zabjek, K. F. (1996). Unified theory regarding A/P and M/L balance in quiet stance. *Journal of Neurophysiology, 75,* 2334-2343.

Woollacott, M., Debu, B., & Mowatt, M. (1987). Neuromuscular control of posture in the infant and child: Is vision dominant? *Journal of Motor Behavior, 19,* 167-186.

Woollacott, M. H., Shumway-Cook, A., & Nashner, L. M. (1986). Aging and posture control: changes in sensory organization and muscular coordination. *International Journal of Aging & Human Development, 23,* 97-114.

Yang, J. F., Winter, D. A., & Wells, R. P. (1990). Postural dynamics in the standing human. *Biological Cybernetics, 62,* 309-320.

Zatsiorsky, V. M. & Duarte, M. (1999). Instant equilibrium point and its migration in standing tasks: Rambling and trembling components of the stabilogram. *Motor Control, 3,* 28-38.

Zatsiorsky, V. M. & Duarte, M. (2000). Rambling and trembling in quiet standing. *Motor Control, 4,* 185-200.